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REVISION OF *ERIGERON* SECT. *LINEARIFOLII* (ASTERACEAE: ASTEREAE)

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ABSTRACT

In a taxonomic study of *Erigeron foliosus* and its close relatives (sect. *Linearifolii*), fourteen species are recognized: *E. aequifolius*, *E. angustatus*, *E. biolettii*, *E. blochmaniae*, *E. breweri*, *E. elmeri*, *E. foliosus*, *E. inornatus*, *E. mariposanus*, *E. miser*, *E. oxyphyllus*, *E. petrophilus*, **E. reductus** *comb. et stat. nov.*, and **E. serpentinus** *sp. nov.* Seven varieties are recognized in *E. breweri*: var. **bisanctus** *var. nov.*, var. *breweri*, var. **covillei** *comb. nov.*, var. **ensenadensis** *var. nov.*, var. *jacinteus*, var. *porphyreticus*, and var. **klamathensis** *var. nov.* Five varieties are recognized in *E. foliosus*: var. *confinis*, var. *foliosus*, var. **franciscensis** *var. nov.*, var. *hartwegii*, and var. **mendocinus** *comb. et stat. nov.* Three varieties are recognized in *E. inornatus*: var. **calidipetris**, *var. nov.*, var. **keilii** *var. nov.*, and var. *inornatus*. Three varieties are recognized in *E. petrophilus*: var. *petrophilus*, var. **viscidulus** *comb. nov.*, and var. **sierrensis** *var. nov.* Most of these have the greatest part of their range in California, from there extending eastward into Nevada, southward into Baja California, and northward to Washington. *Erigeron oxyphyllus* E. Greene is restricted to southern Arizona and adjacent Sonora. A detailed taxonomic treatment, including nomenclature and distribution maps, is provided for these taxa. Five other species peripherally related to the *E. foliosus* group are more briefly treated: *Erigeron hyssopifolius* of the northeastern United States and adjacent Canada; *E. chiangii* and *E. scoparioides* from northeastern México; and *E. rhizomatus* and *E. lepidopodus* from northwestern México and the southwestern United States.

KEY WORDS: *Erigeron*, Astereae, Asteraceae, California

The group of taxa including *Erigeron foliosus* Nutt., *E. breweri* A. Gray, and *E. inornatus* (A. Gray) A. Gray has long been known to show complex

patterns of variation. Compton (1934) published a short study of the *E. foliosus* complex in a narrow sense, but the group was treated in full by Cronquist (1947) in his revision of the 133 North American species known at that time. A partial summary of Cronquist's view of the taxonomy of this group is seen in his comment (1947, p. 281) that "The *E. foliosus–E. breweri* complex presents some of the most difficult problems in the genus *Erigeron*. There are a multitude of recognizable forms, often with relatively strong morphological characters, but these interlock and intergrade in such a way that taxonomic segregation becomes difficult, and a completely satisfactory treatment seems impossible." With respect to the group at hand, Cronquist recognized six species, and his delimitations of the taxa have been essentially the only ones in use since then, because he contributed treatments of *Erigeron* consistent with the concepts of his revision to virtually all of the major floristic studies of the Pacific coast since 1947.

The taxonomy presented here differs considerably from that of Cronquist (1947), and this is the first study to include detailed mapping of the geographic ranges of these taxa (Maps 1-9), which provides evidence significant in directing the taxonomic decisions. All taxa recognized by Cronquist, except one, are recognized in the present study, and apart from eight previously unrecognized taxa, the other differences in treatment in large part reflect the recognition of new taxa and the elevation of varietal taxa to the rank of species. Such shifts have resulted from the observation that, in many cases, the taxa involved have discrete morphological and geographical ranges, they are broadly or completely sympatric with putatively conspecific taxa, and intergradation among these taxa is less than previously supposed. As regarded here, a large component of the confusing variation has resulted from previously unrecognized entities as well as parallel tendencies of variability among some of the taxa. Even with this seemingly less conservative approach, it is clear, as also seen by Cronquist, that several of the most widespread species are complex and comprise a number of varieties (*e.g.*, as treated here, *E. foliosus* with five varieties and *E. breweri* with seven varieties).

In previous studies (*e.g.*, Nesom 1990), I have tried to be consistent in the application of names at the varietal rank, referring these to closely similar taxa that are geographically contiguous and intergrading at their zone of contact. In the *Erigeron foliosus* group, however, some of the species comprise sets of allopatric taxa separated by relatively small differences; some of these are intergrading, but the intergradation is more likely the reflection of parallel variability resulting from common ancestry rather than gene flow. A similar pattern of variability has been observed among some of taxa of the *E. eatonii* A. Gray group (Strother & Ferlatte 1989). As has been the trend in the present study, an alternative treatment might consider some of these allopatric population systems with small but distinctive differences as separate species, requiring higher rank for some of the taxa recognized here as varieties (as

noted below).

The present study treats in detail only the taxa of the *Erigeron foliosus* group, which are clearly closely related among themselves. Putatively related species (Nesom 1989) that are geographically and morphologically widely peripheral are briefly included, but these need to be investigated in more detail to determine their degree of relationship. Although the major patterns of variation within the *E. foliosus* group seem to be fairly clear, problems remain in two areas: (1) the definition of some of the taxa (particularly within *E. breweri* and *E. petrophilus* E. Greene), for which field work in specific geographic areas will be critical in future studies, and (2) the pattern of phylogenetic relationships among the taxa. I have more confidence that the taxa recognized here are real entities in nature than I do that they are related as proposed. With further detailed examination, the taxonomy advanced here will almost certainly be modified.

The concepts presented in this study are derived from examination of more than 2000 specimens, representing the whole geographic range of the group, although the taxa are primarily centered in California. Using the keys and distribution maps, identifications can be made with relative confidence. The nature of the characters that delimit the varietal taxa, however, will be easier to interpret with reference specimens for comparison.

Chromosome counts have been made for eleven of the taxa included here (as documented below; all recorded here in "gametophytic" form, regardless of how they were reported). All of the taxa counted, except one of the peripheral species, are diploid. The discovery that polyploids were more common would not be unexpected, since they are known to be common in *Erigeron* even within single species without taxonomic subdivision. Their presence, however, in whatever pattern, would probably not alter the taxonomic structure presented here.

The taxa are treated alphabetically. Authorships for all names mentioned in the text can be found in the formal nomenclature. Designations of geographic provinces in California follow Hickman (1989). Specimens are cited for new or rare taxa and elsewhere when necessary to clarify critical differences with previous taxonomic treatments. Taxa that are more common and more easily recognized are documented by detailed mapping; a single symbol may represent numerous collections for commonly collected taxa.

Erigeron sect. *Linearifolii* (G. Don) Nesom, Phytologia 67:79. 1989.

Erigeron sect. *Linearifolii* (G. Don) Nesom, Phytologia 67:79. 1989. BASIONYM: *Aster* sect. *Linearifolii* G. Don *in* Loudon, *Hort. Brit.* 346. 1830. LECTOTYPE (Sundberg & Jones 1987): *Aster graminifolius* Banks *ex* Pursh (= *Erigeron hyssopifolius* Michx.). Sundberg & Jones (1987) lectotypified *Aster* sect. *Linearifolii* with *A. graminifolius*. Their

choice of a type was apparently intended solely to preserve an established name within the genus *Aster*. Without an understanding of the taxonomy of *Erigeron*, however, they merely transferred the problem from one genus to another (*Aster* to *Erigeron*). See comments below regarding the relationship of *E. hyssopifolius* to the *E. foliosus* group).

Erigeron sect. *Pycnophyllum* Cronq., Brittonia 6:141. 1947. TYPE: *Erigeron foliosus* Nutt. (see additional comments following *E. hyssopifolius* regarding *Erigeron* sect. *Linearifolii*).

Perennial herbs, glandular or eglandular, with or without eglandular vestiture, the stems prostrate or sprawling to decumbent ascending or erect, arising from fibrous rooted rhizomes or a woody taproot. Leaves all cauline, filiform to oblanceolate, entire, usually densely arranged and markedly longer than the internodes, not reduced upwards. Heads solitary or few in corymboid clusters; phyllaries strongly graduated in 3-5 series, usually with a strongly orange resinous midrib, rarely with 3 parallel veins; receptacles smooth to shallowly foveolate. Ray flowers absent or present in a single series, the corollas white or drying bluish, at maturity often slightly coiling at the tips. Disc corollas numerous, narrowly funnelform, the lower half sometimes slightly indurated; style branches with shallowly triangular collecting appendages ca. 0.1 mm long. Achenes compressed, with 2(-4) strongly orange resinous ribs, the surfaces usually shiny; pappus mostly of 20-35(-50) bristles, usually with a few, outer setae. Chromosome numbers, n=9, 18.

Plants of this section are recognized particularly by the long, ascending, decumbent, or prostrate basal portions of their stems, the narrow (usually), entire, and densely arranged cauline leaves, lack of persistent basal leaves, graduated phyllaries, minute collecting appendages of the disc style branches, and achenes with shiny surfaces and strongly orange resinous ribs. Further, the heads are solitary in some taxa, but they typically are more numerous and occur at the tips of branches arising near the apex of the stems, strongly reminiscent of the capitular arrangement in *Heterotheca* and *Chrysopsis*. Sect. *Linearifolii* has radiated almost exclusively within the boundaries of California; only two of the taxa lie completely outside of the state (one in Arizona and one in northwest México); several extend to the south into Baja California, east into Nevada, and north into Oregon and Washington.

KEY TO THE SPECIES OF THE *ERIGERON FOLIOSUS* GROUP OF SECT. *LINEARIFOLII*

1. Ray flowers absent. ..... (9)

1. Ray flowers present. ..... (2)

2. Stem vestiture a mixture of eglandular and minutely but distinctly stipitate glandular hairs. ..... *E. aequifolius*

2. Stem vestiture various, but without stipitate glandular hairs. ..(3)

3. Stems essentially glabrous to sparsely strigose with short, straight, ascending-appressed hairs. .....(5)

3. Stem vestiture pubescence short villous or hirsute to hirsutulous, often densely so, with spreading to spreading-deflexed hairs. .....(4)

4. Stem vestiture puberulous to closely villosulous with crinkly hairs; achenes glabrous. .....*E. blochmaniae*

4. Stem vestiture densely hirsutulous with straight, stiffly spreading, usually slightly deflexed hairs; achenes strigose. ..... *E. breweri*

5. Stems with axillary tufts of small leaves at most nodes; phyllaries with prominent, broad, scarious margins. ..... *E. mariposanus*

5. Stems without axillary tufts of small leaves; phyllaries without prominent scarious margins. .....(6)

6. Stems prostrate to decumbent trailing, arising from slender, fibrous rooted rhizomes. ..... *E. elmeri*

6. Stems basally ascending but essentially erect, arising from a woody taproot. .....(7)

7. Middle and upper leaves much shorter than the internodes, eciliate. ....*E. oxyphyllus*

7. Middle and upper leaves much longer than the internodes, ciliate with ascending-appressed hairs. .....(8)

8. Leaves ciliate with thick based hairs; phyllaries usually with conspicuous eglandular hairs, rarely glandular; ray flowers 15-50. ....*E. foliosus*

8. Leaves ciliate with thin based hairs; phyllaries with barely perceptible eglandular hairs, densely granular glandular; ray flowers 9-13. . .....*E. serpentinus*

9. Leaves oblanceolate; stems with long ascending basal portions arising from a woody taproot. .....(11)

9. Leaves linear; stems erect from the base, arising directly from a multicipital rootcrown, or arising from slender, rhizomelike caudex branches. .(10)

10. Stems 30-90 cm tall, basally erect, numerous, arising directly from a strongly woody rootcrown. ..... *E. angustatus*

10. Stems 8-20(-30) cm tall, basally erect or ascending, usually few and arising singly from thin, rhizomelike, caudex branches. *E. reductus*

11. Phyllaries eglandular. ..... *E. inornatus*

11. Phyllaries glandular. ..... (12)

12. Eglandular hairs on at least the lower half of the stems spreading. ..... (14)

12. Eglandular hairs of the stems sparse and antrorsely appressed or completely absent. ..... (13)

13. Upper stems and leaves glandular. ..... *E. biolettii*

13. Upper stems and leaves eglandular. ..... *E. inornatus*

14. Stems and leaves eglandular. ..... (15)

14. At least the upper stems and leaves distinctly glandular, sparsely to densely hirsute-villous with long, somewhat crinkly spreading hairs. ..... (16)

15. Stems densely hirsutulous with short, slightly deflexed hairs of even length, or the hairs sometimes loosely antrorsely ascending. ..... *E. inornatus* var. *keilii*

15. Stems sparsely hispid-pilose with long, stiffly spreading hairs, or the hairs sometimes antrorsely ascending-appressed. *E. petrophilus* var. *viscidulus*

16. Stems 30-90 cm tall, erect; leaves 20-40 mm long; heads 12-15 mm wide. ..... *E. biolettii*

16. Stems 5-20(-30) cm tall, basally ascending or decumbent; leaves 7-25 mm long; heads 7-12 mm wide. ..... (17)

17. Inner phyllaries (3.5-)4.0-5.0 mm long. ..... *E. miser*

17. Inner phyllaries 5.5-7.0 mm long. ..... *E. petrophilus*

1. *Erigeron aequifolius* H.M. Hall

Erigeron aequifolius H.M. Hall, Univ. Calif. Publ. Bot. 6:174. 1915. TYPE: UNITED STATES. California: Tulare Co., ridges at Trout Meadows, Transition Zone, 6200 ft, 16 Jul 1908, *H.M. & G.R. Hall 8386* (HOLOTYPE: UC!; Isotypes: GH!,UC!,US!).

Stems ascending-erect, 10-20 cm long, from slender, woody, rhizomelike caudex branches. Stems and leaves minutely granular glandular, sparsely short villous. Leaves narrowly elliptic to oblanceolate, 6-20 mm long, 1.5-3.0 mm wide. Heads 7-10 mm wide; phyllaries minutely glandular, sometimes with a few other nonglandular hairs at the base, inner phyllaries 3.5-4.0 mm long. Ray flowers 14-24(-30), the corollas 5-8 mm long, drying blue. Disc corollas (2.8-)3.8-4.5 mm long. Achenes 2.2-2.5 mm long; pappus bristles 20-35. Chromosome number, n=9 (Semple 1985).

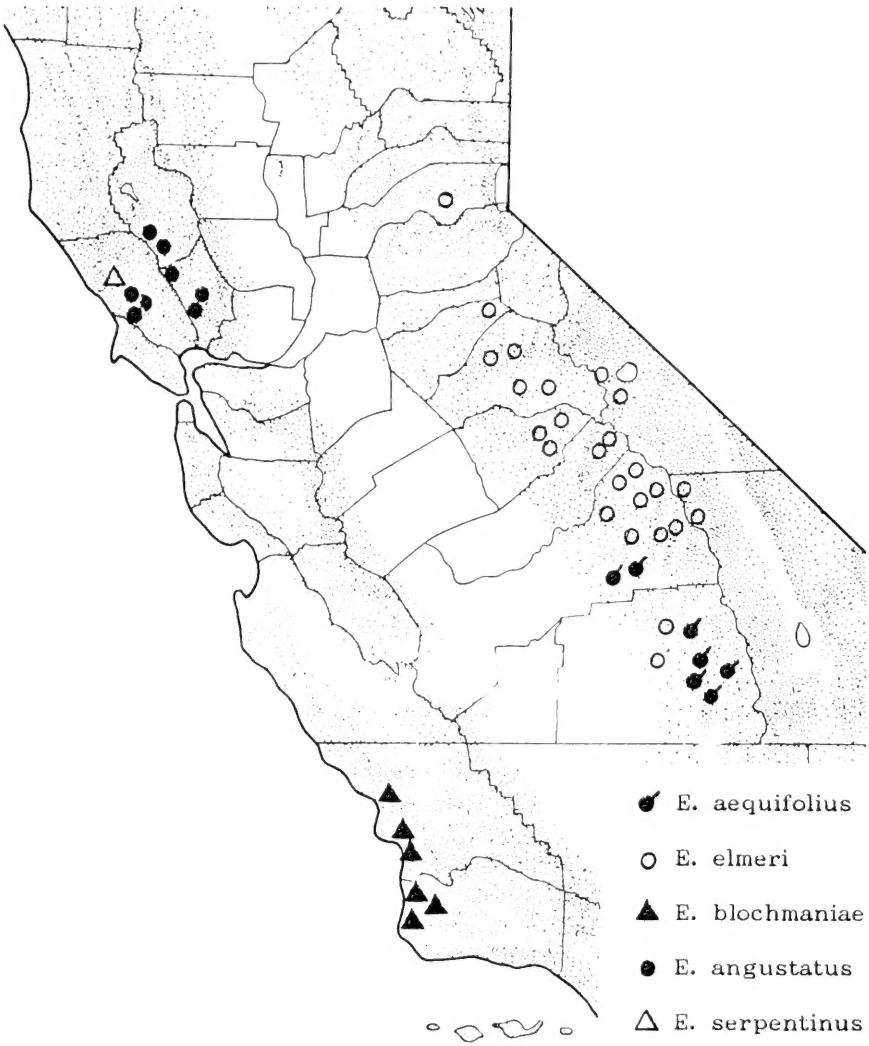
California endemic, southern High Sierra Nevada (Map 1); ledges, crevices, 1560-2010 m; Jul-Aug.

Cronquist's prophecy regarding the potential validity of *Erigeron aequifolius* (1947) has held true. The species is now known by a number of collections of morphologically consistent plants, none of which show intermediacy with any other species. It probably is most closely related to *E. breweri*, with which it is completely sympatric, and to *E. elmeri* (E. Greene) E. Greene, with which it is partially sympatric.

2. *Erigeron angustatus* E. Greene

Erigeron angustatus E. Greene, Bull. Calif. Acad. Sci. 1:88. 1885. TYPE: UNITED STATES. California: Napa Co., "dry hills on either side of Napa Valley, Jul-Oct" [Napa, 13 Aug 1874], *E. Greene 339* (not located; probable duplicate: GH!). Although the type of *E. angustatus* is the same as one of the syntypes of *E. inornatus* A. Gray var. *angustatus* A. Gray (= *E. reductus* [Cronq]. Nesom var. *angustatus* [A. Gray] Nesom in the present study), there is no indication that Greene intended his name as a new combination based on Gray's earlier one. None of the sheets of this taxon at ND-G (cited below), all identified by Greene as *E. angustatus*, appear to be type material. I have not designated the GH specimen as lectotype, because I believe Greene's original collection eventually will be located.

Stems 3-9 dm tall, erect, arising directly from the crown of a thick taproot. Stems and leaves mostly glabrous, the margins widely and sparsely ciliate. Leaves linear, 1-6 cm long, 0.5-1.0(-2.0) mm wide. Heads 8-12 mm wide; phyllaries granular-glandular, without other vestiture, the inner 5.5-7.5 mm



Map 1. *Erigeron aequifolius*, *E. elmeri*, *E. blochmaniae*, *E. angustatus*, and *E. serpentinus*.

long, usually purple at the apex. Ray flowers absent. Disc corollas 4.2-6.0 mm long. Achenes 2.4-2.8 mm long; pappus bristles 26-38.

California endemic, southern Outer North Coast Ranges (Map 1); serpentine areas, often in loose rocks, usually in brushy vegetation, ca. 90-150 m; May-Sep.

Additional collections examined: UNITED STATES. California: Lake Co., no other locality data, 15 May 1893, *Blankenship s.n.* (UC); Whispering Pines Resort, 30 Jun 1940, *Baker 9743* (CAS,UC); foot of "Rabbit Hill," just SW of center of Middletown, 17 Aug 1971, *Hamann & Dearing s.n.* (JEPS). Napa Co.: St. Helena, 10 Jul 1891, *E.L. Greene s.n.* (ND-G 4 sheets); E side of Mt. St. Helena, 24 Aug 1941, *Hoover 5572* (JEPS); Sage Canyon, Napa Range, 27 Aug 1933, *Howell 11625* (CAS); Soda Creek Canyon, Napa Valley between Napa City and Yountville, 7 Aug 1938, *Tracy 16089* (DS,LL,UC). Sonoma Co.: Cazadero, side of stream, 24 Jun 1943, *Cooke s.n.* (UC); Dutch Bill Creek, 5 Sep 1947, *Hoffman 1249* (UC); between Occidental and Graton, 26 Jul 1936, *Howell 12669* (CAS); 2 mi E of Occidental, 5 Jul 1946, *Mason & Grant 12898* (UC).

This narrowly endemic species has not been recognized since its original description by Greene, but it is distinctive in morphology and habitat. It was included by Cronquist (1947) with *Erigeron inornatus* var. *angustatus* (*E. reductus* var. *angustatus* in the current study), which produces stems that are stolonlike and nearly filiform at the base, with no well developed root crown. *Erigeron angustatus* also has been confused with *E. biolettii* E. Greene, which is eradiate and somewhat similar in habit, though different in vestiture and habitat. The stems and leaves of *E. angustatus* are glabrous (vs. glandular), the leaves narrower (mostly linear and 0.5-1.0 mm vs. narrowly oblanceolate and 2-4 mm wide), and the stems arise directly and erect from the crown, in contrast to the long, ascending basal portions that are characteristic of *E. biolettii*. The two taxa are partially sympatric, and no intermediates have been seen in this study. Additional comments are given following *E. reductus* and *E. serpentinus* Nesom.

3. *Erigeron biolettii* E. Greene

Erigeron biolettii E. Greene, *Man. San Franc. Bay Region* 181. 1894. LECTOTYPE (Cronquist 1947): UNITED STATES. California: Sonoma Co., base of Hood's Peak, 8 Jul 1892, *F.T. Biolett s.n.* (ND-G!). *Erigeron inornatus* (A. Gray) A. Gray var. *biolettii* (E. Greene) Jeps., *Fl. W. Mid. Calif.* 569. 1901. Greene also cited a collection from Howell Mt. (Napa Co.) by Jepson.

Stems 3-9 dm tall, erect or the basal portions usually long, ascending, and somewhat caudexlike, usually purplish at the base. Stems and leaves

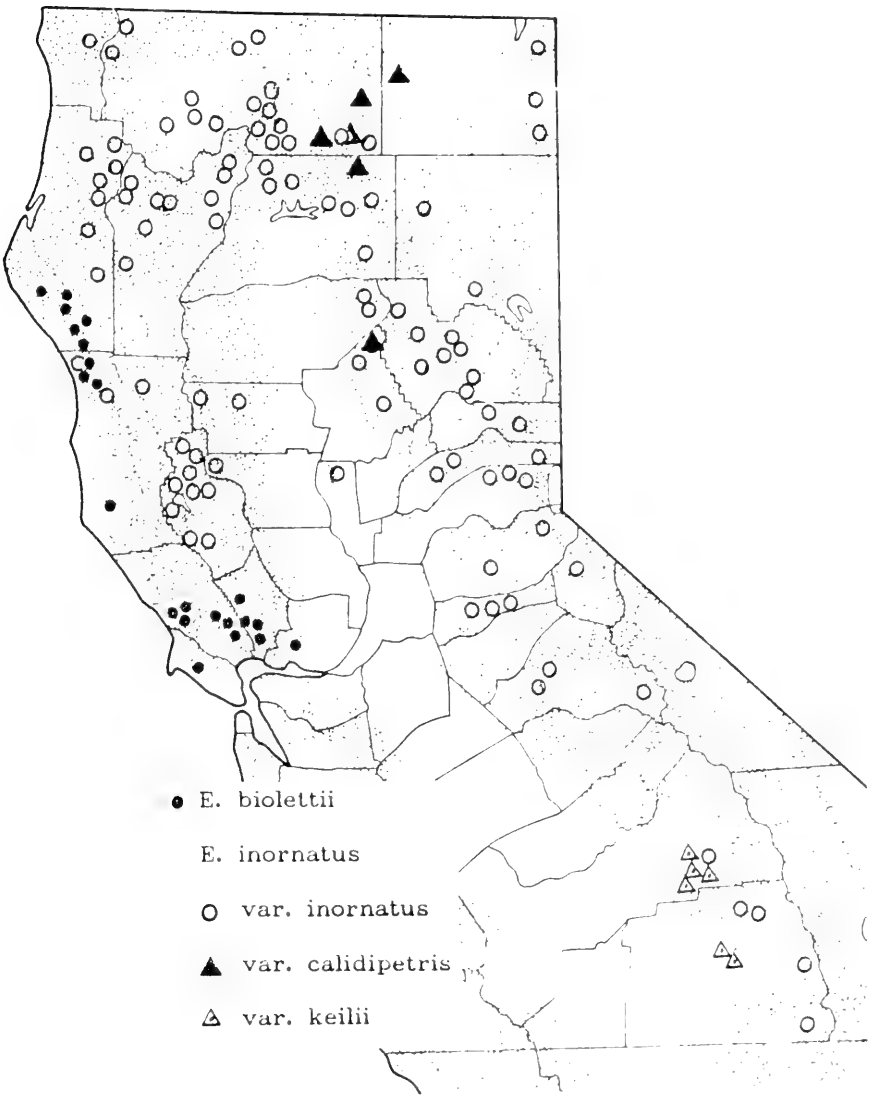
densely glandular, often also sparsely hispid or hispid-pilose. Leaves narrowly oblanceolate, 2-4 cm long, 2-4(-5) mm wide. Heads 12-15 mm wide; phyllaries densely glandular, the inner 6.0-8.0 mm long, usually purple at the apex. Ray flowers absent. Disc corollas 4.5-6.5 mm long. Achenes 2.0-2.5 mm long; pappus bristles 22-38.

California endemic, Outer North Coast Ranges (Map 2); dry slopes, rocks and ledges along rivers, 30-700(-1030) m; Jun-Sep.

Representative collections examined: UNITED STATES. California: Humboldt Co.: Mattole River at Union Mattole, 4 Aug 1929, *Kildale 8777* (DS-2 sheets); 5 mi N of Mendocino-Humboldt county line, S. Fork of Eel River, 9 Aug 1936, *Munz 14331* (UC); Humboldt Co. State Park, Eel River, 9 Jul 1923, *Peirson 3877* (UC); along S. Fork Eel River, 3-5 mi above its mouth, 23 Jul 1912, *Tracy 3797* (UC); near Garberville, along S. Fork Eel River, 9 Sep 1933, *Tracy 13076* (UC). Marin Co.: Pt. Reyes P.O., Jul 1903, *Elmer 4649* (DS,MO). Mendocino Co.: Red Mt., 15 Jul 1969, *Gankin et al. 2666* (CAS); along Eel River at Richardson (redwood) grove, 26 Jul 1924, *Heller 13887* (DS,MO); Hale's Camp, near Redwood Highway, 14 Jul 1931, *Jones 29145* (UC); Navarro River near Philo, 11 Jul 1909, *McMurphy 512* (DS); Red Mountain Creek Bluff, on S. Fork Eel River, 8 mi S of north county boundary, 7 Aug 1938, *Tracy 16100* (DS,UC). Napa Co.: near St. Helena Sanitarium, 2 Jul 1916, *Abrams 5750* (DS); Howell Mountain, Aug 1888, *T. Brandegee s.n.* (UC); Alta Loma Ranch, 7-14 Sep 1906, *Chandler 7134* (UC); Howell Mt., Napa River Basin, 1893, *Jepson s.n.* (JEPS); ridge SE of Mt. Veeder, 21 Aug 1951, *Raven 9867* (CAS). Solano Co.: Cordelia, 17 Aug 1920, *Campbell s.n.* (CAS); Stone Quarry Hill, Cordelia, 7 Aug 1901, *Jepson 1743* (JEPS). Sonoma Co.: near summit of Mt. Hood, 27 Jul 1948, *Baker 12079* (CAS); Hope Val at summit above Coleman's Ranch, near Kenwood, Aug 1950, *Baker 12309* (UC); Russian River, below Guerneville, 22 Jul 1896, *Davy 4147* (UC); Guernewood Park, 25 Jun 1909, *Hall 8518* (DS-2 sheets,MO,UC); Sonoma Creek Canyon near Kenwood Springs, 9 Oct 1932, *Howell 10811* (CAS); dry hills near Agua Caliente, 1 Aug 1933, *Jepson 16551* (JEPS); Duncan's Mills, 17 Jul 1882, *Jones 3620* (CAS,DS-2 sheets,MO,UC).

Plants of the northern segment of the range of *Erigeron biolettii* (Map 2) produce slightly broader leaves more densely arranged on the stems than those of the southern segment. The differentiation appears to be so slight, however, that there is no justification for applying more than a single name. Collections identified by Cronquist (1947) as *E. biolettii* from Tuolumne and Fresno counties are slightly glandular plants of *E. inornatus*.

Of the varieties of *Erigeron inornatus* maintained by Cronquist (1947), *E. biolettii* might be held at that rank more justifiably than the others. The few collections, however, that might be interpreted as intermediate between *E. inornatus* and *E. biolettii* (e.g., *Tracy 16100*) occur where they apparently are closely sympatric in a small area of northern Mendocino Co., in contrast to



Map 2. *Erigeron inornatus* and *E. biolettii*. The range of var. *inornatus* extends through Oregon into southcentral and southeastern Washington, and into immediately adjacent Nevada.

their otherwise relatively wide geographic ranges.

The stems and leaves of *Erigeron biolettii* are always glandular, but eglandular hairs range from absent to present in variable densities. The vestiture of plants of a few collections even appears to approach that of *E. petrophilus*, but the two species are distinct in habit. *Erigeron biolettii* is also similar to *E. angustatus* and partly sympatric with it, but the latter has linear leaves and is glabrous or nearly so.

4. *Erigeron blochmaniae* E. Greene

Erigeron blochmaniae E. Greene, Pittonia 3:25. 1896. LECTOTYPE (Cronquist 1947): UNITED STATES. California: Santa Barbara Co., Santa Maria, beach and sand a few miles inland, "summer," *I.M. Blochman s.n.* (ND-G!). *Erigeron foliosus* Nutt. var. *blochmaniae* (E. Greene) H.M. Hall, Univ. Calif. Publ. Bot. 3:91. 1907. Greene cited no specimens in the original description, but the ND-G sheet selected fits the protologue and was marked "Type" by Greene.

Stems 4-8 dm tall, erect or usually ascending and caudexlike at the base (some labels note a "rhizomatous" habit). Stems and leaves densely and closely puberulous to villosulous with minute, stiffly crisped hairs. Leaves linear to narrowly oblanceolate, 1.5-3.0 cm long, 1-3 mm wide. Heads 9-14 mm wide; phyllaries densely glandular and densely canescent-hirsutulous, linear-lanceolate, with a broad orange middle area and thick, white lateral zones, the inner 4.5-6.0 mm long. Ray flowers 45-72, the corollas 8-11 mm long, drying white to blue. Disc corollas 4.6-5.0 mm long. Achenes 2.2-2.8 mm long; pappus bristles 21-36. Chromosome number, n=9 (Keil *et al.* 1988).

California endemic, Central Coast in San Luis Obispo and Santa Barbara cos. (Map 1); sand dunes and hills, 3-30 m; Jul-Oct.

Cronquist (1947) observed that this taxon might justifiably be treated as a separate species but kept it within *Erigeron foliosus* because of putative intergradation with var. *foliosus*. The specimens that may have been regarded as intermediates were perhaps those treated here as *E. foliosus* var. *franciscensis* Nesom (discussed further following the latter), which among the varieties of *E. foliosus* is most similar to *E. blochmaniae*, but these two taxa do not intergrade. *Erigeron blochmaniae* is restricted to the coastal sands of Santa Barbara and San Luis Obispo counties and is recognized particularly by its large heads, distinctive stem vestiture, and completely glabrous achenes.

5. *Erigeron breweri* A. Gray

Erigeron breweri A. Gray, Proc. Amer. Acad. Arts 6:541. 1865. LECTOTYPE (designated here): UNITED STATES. California: Mariposa Co.,

Yosemite Valley, 4000 ft, 1863, *W.H. Brewer 1651* (GH; Isolectotypes: UC!,US!; Probable isolectotypes: UC-2 sheets). Gray also cited in the protologue a collection from Nevada (*C.L. Anderson 94132*-GH). Cronquist (1947) cited only the Brewer collection but apparently saw only the US specimen.

Stems ascending-erect, 20-75 cm long, arising from slender, rhizomelike or caudexlike branches, usually densely invested (sparsely in var. *klamathensis*) with short, even length, spreading-deflexed hairs, eglandular. Leaves linear to narrowly oblanceolate or oblanceolate, entire, 5-40 mm long. Heads 8-15 mm wide, in a terminal cluster; phyllaries glandular, sometimes also with nonglandular hairs. Ray flowers 12-45, the corollas 4-7 mm, drying blue, less commonly white to pink. Disc corollas 3.5-6.0 mm long. Achenes 2.2-2.8 mm long; pappus bristles 22-46.

Key to the varieties of *E. breweri*

1. Phyllaries densely glandular, nonglandular hairs lacking or very sparse. . . . . (2)

1. Phyllaries slightly glandular to eglandular, with prominent nonglandular hairs. . . . . (4)

2. Stems prostrate to procumbent or decumbent, 7-15 cm; leaves 5-12 mm long. . . . . var. *jacinteus*

2. Stems commonly basally ascending but the upper portions erect, usually longer than 20 cm; leaves mostly longer than 15 mm. . (3)

3. Hairs of stems and leaves 0.1-0.2 mm long; inner phyllaries with green, *Aster*-like apical areas; stems arising from slender, fibrous rooted, rhizomelike bases, without a strongly developed woody root. . var. *breweri*

3. Hairs of stems and leaves 0.5-1.0 mm long; inner phyllaries with broad, white thickened margins, lacking a distinctly demarcated, green apical area; stems arising from slender but woody basal offsets, these from a strongly developed, woody root. . . . . var. *klamathensis*

4. Stems 20-30 cm, distinctly wiry and brittle; phyllaries with long, thick based, stiffly spreading, translucent hairs, distinctly glandular as well. . . . . var. *porphyreticus*

4. Stems (30-)40-75 cm, thickening toward the base, not wiry or brittle; phyllaries with short, white, ascending to appressed hairs, eglandular. . . . . (5)

5. Hairs of stems and phyllaries barely longer than broad; plants of Baja California Norte. ..... var. *ensenadensis*

5. Hairs of stems and phyllaries longer; plants of California. .....(6)

6. Phyllaries with thick based, ascending hairs, the hairs dense on the outermost, sharply reduced in density on the middle and inner. .. . . var. *covillei*

6. Phyllaries with thin based, appressed-ascending hairs, the hairs gradually and slightly reduced in density from the outer toward the inner. ..... var. *bisanctus*

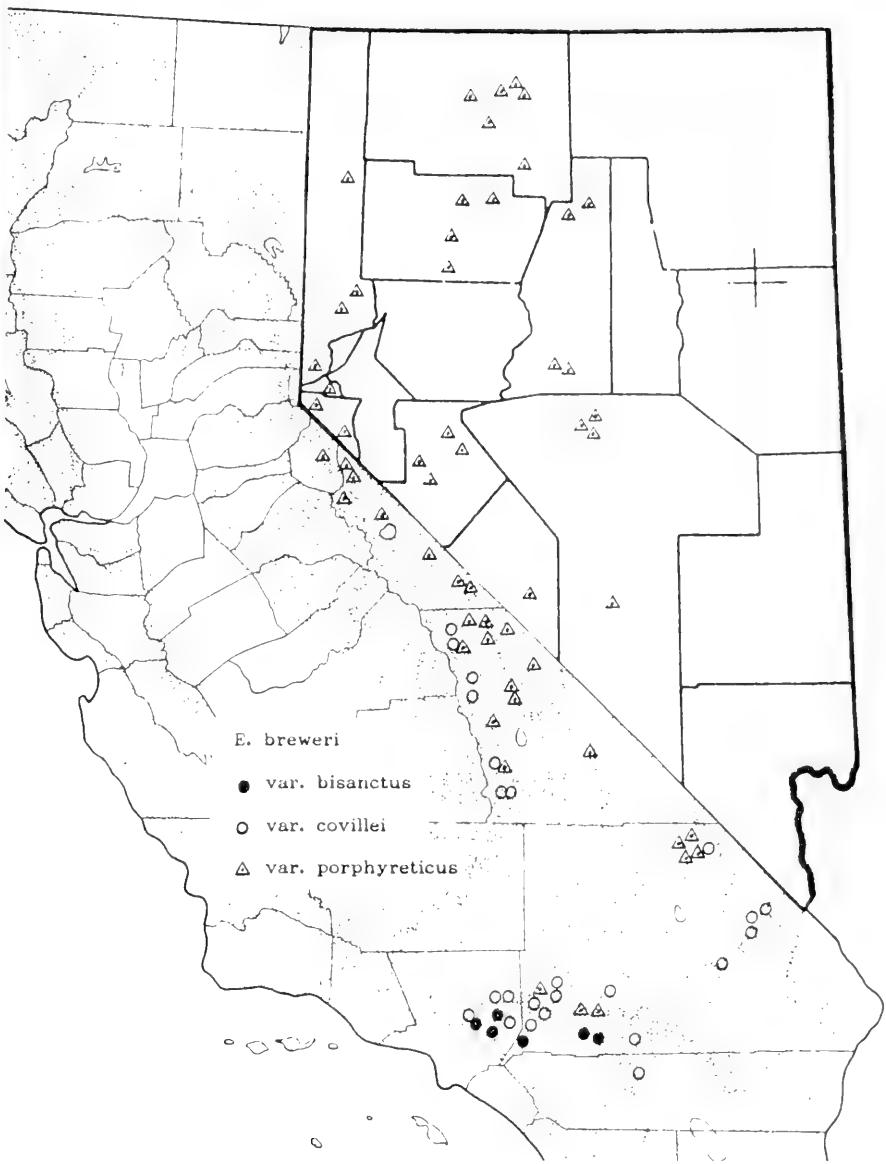
a. **Erigeron breweri** A. Gray var. **bisanctus** Nesom, *var. nov.* TYPE: UNITED STATES. California: Los Angeles Co., San Antonio Canyon near Claremont, 2 Aug 1903, *C.F. Baker 3451* (HOLOTYPE: LL!; Isotypes: CAS!,UC!). These specimens were distributed as a new species proposed by E.L. Greene, using the epithet "*antoninus*," which was apparently never validly published. An additional sheet of *Baker 3451* (CAS) bears a plant of *E. foliosus* var. *foliosus*.

Erigeronti breweri A. Gray var. *covillei* (E. Greene) Nesom similis sed phyllariis trichomatibus appressis ad basim tenuibus vestitis differt.

California endemic, San Gabriel and San Bernardino Mts. (Map 3); open, dry slopes and washes, 370-1520 m; May-Sep.

Additional collections examined: UNITED STATES. California: Los Angeles Co.: San Antonio Canyon, 2 Aug 1903, *Baker 3658* (LL,UC); San Dimas and San Gabriel Divide, Cucamonga Quad., 20 Sep 1935, *Horton 248* (UC); San Gabriel Canyon, 28 Jun 1892, *Hutchinson s.n.* (JEPS). San Bernardino Co.: 5 mi NE of Upland, 14 Jun 1927, *Blake 9867* (LL); E fork of the Santa Ana River, 3 mi below CA Hwy 38, 9 Jul 1974, *Helmkamp s.n.* (UCR); Santa Ana River, 28 Aug 1922, *Munz 6332* (UC-2 sheets); San Gabriel Mts., Big Dalton Canyon, chaparral, 10 Jun 1984, *Swinney s.n.* (UCR); 2 mi E of Claremont, 28 May 1933, *Wheeler 1748* (LL); Santa Ana River drainage, Forest Service Road 1N64, between the 2 forks of Deer Creek, 18 Jul 1990, *White s.n.* (TEX,UCR).

These plants have tall, thick, and relatively unbranched (until the capitulescence, near the apex) stems similar to var. *covillei*, but the phyllaries are densely invested with thin based, appressed hairs distributed somewhat differently. The two apparently grow in close proximity (e.g., *Baker 3658* [MO] from the San Antonio Canyon, the type locality of var. *bisanctus*, is var. *covillei*).



Map 3. *Erigeron breweri* (var. *porphyreticus*, var. *covillei*, and var. *bisanctus*).

Some plants of *Erigeron foliosus* in the the same region have phyllaries with vestiture nearly identical to var. *bisanctus*, and seems probable that gene flow occurs between these two taxa.

b. *Erigeron breweri* A. Gray var. *breweri*

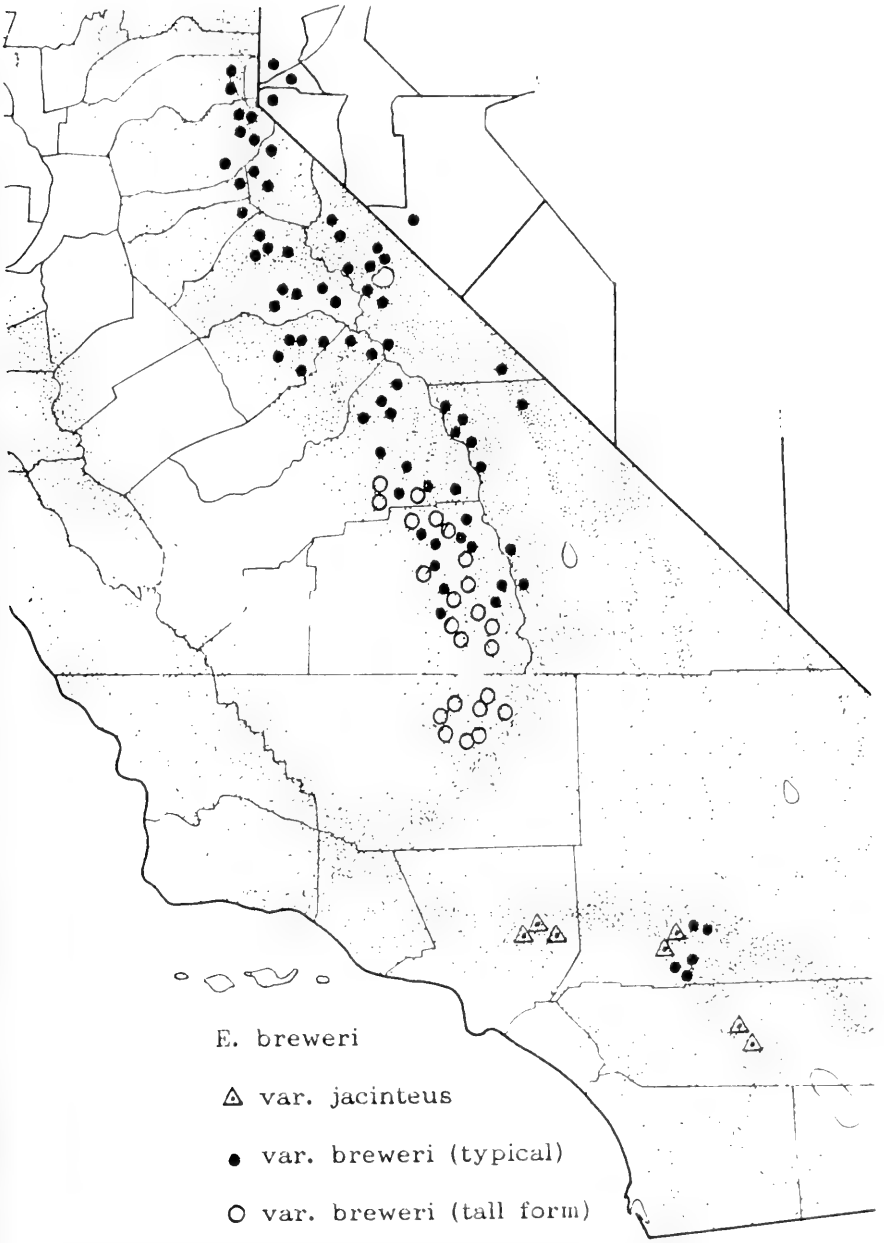
Chromosome number, n=9 (Solbrig *et al.* 1969; Semple *et al.* 1989).

California, northern to southern High Sierra Nevada, Nevada in the Lake Tahoe region, apparently disjunct in the San Bernardino Mts. (Map 4); open, rocky sites in a variety of vegetation types, (1220-)1800-2930(-3050) m; Jun-Sep.

As interpreted here, var. *breweri* has a discrete geographic distribution in the eastcentral Sierra Nevada, with an outlying segment to the southwest in the San Bernardino Mountains. It remains one of the most complex taxa of the section, deserving further study and perhaps ultimately better treated as two varieties rather than one. Plants of the typical form produce thin, woody rhizomes with relatively short (12-40 cm), ascending stems and the leaves are distinctly oblanceolate. In Fresno and Tulare cos., many of the plants produce thicker stem bases, taller (30-60 cm) and more erect stems, and more linear leaves; only the tall form is present at the southern extremity of the range in Kern Co. The two forms are mapped with different symbols (Map 4), although many of the determinations are arbitrary in Fresno and Tulare cos., where the intergradation seems to be gradual. The taller plants were included by Cronquist (1947) in var. *covillei*, but while they have its habit, perhaps reflecting the genetic influence of that variety, they produce the relatively shorter, merely glandular phyllaries distinctive of var. *breweri*. Further, their sierran habitats and range, together with their apparent complete intergradation with the typical form, make it difficult to virtually impossible to recognize more than a single taxon.

The plants identified as var. *breweri* from the San Bernardino Mountains are most like the typical form, apparently long disjunct from the main range. They apparently occur in several localities, but a number of collections have been made from along the South Fork of the Santa Ana River and in the vicinity of Bear Valley. A collection of typical var. *breweri* (CAS, on the label: Mt. Eddy, Jul 1880, *Lemmon s.n.*) is almost certainly mislabeled, as no other collection of that taxon has been made anywhere near Siskyou County. This collection of var. *breweri* may have been made in the vicinity of Mt. Lassen (see additional comments following var. *klamathensis*).

c. **Erigeron breweri** A. Gray var. **covillei** (E. Greene) Nesom, *comb. nov.* BASIONYM: *Erigeron covillei* E. Greene, Erythea 3:20. 1895. LECTOTYPE (designated here): UNITED STATES. California: Inyo Co.,



Map 4. *Erigeron breweri* (var. *breweri* - the typical form and the "tall form" are mapped with different symbols - and var. *jacinteus*).

near Crystal Spring, Coso Mountains, 12 Jun 1891, *F.V. Coville & F. Funston 931* (ND-G!; Isolectotypes: UC-fragment [as cited by Cronquist 1947], US!). *Erigeron foliosus* Nutt. var. *covillei* (E. Greene) Compton, Bull. So. Calif. Acad. Sci. 33:51. 1934.

California endemic, eastern margin of the Sierra Nevada, Mojave Desert, San Gabriel Mts., San Bernardino Mts., San Jacinto Mts. (Map 3); open, rocky sites in sagebrush, chaparral, and juniper, 980-1830 m; May-Sep.

In the view of the present treatment, the dense, spreading-deflexed stem pubescence of these plants places them with *Erigeron breweri* rather than *E. foliosus*. Further, they are broadly sympatric with *E. foliosus* var. *foliosus* and few if any unequivocal intermediates have been seen. Two collections from the area of Independence in Inyo County, otherwise similar to var. *covillei*, are unusual in their *foliosus*-like, antrorsely appressed-ascending stem pubescence: *Raven 9946* (JEPS) and *Alexander & Kellogg 2974* (LL-3 sheets, MO,UC). Intergrades between var. *covillei* and *E. breweri* var. *breweri*, however, were noted by Cronquist (1947) as well as in the present study. Var. *covillei* is strictly a taxon of the Mojave Desert, forming a southern segment of the range of *E. breweri* (Map 3). It is clearly separated from the southern end of the range of var. *breweri*, but intermediates appear to occur with the "tall form" in the Independence Creek area of Inyo County. The possible influence of var. *covillei* on var. *breweri* is discussed following the latter. In addition, where the range of var. *covillei* meets that of var. *porphyreticus* in San Bernardino Co., there are apparent intermediates between them.

d. **Erigeron breweri** A. Gray var. **ensenadensis** Nesom, *var. nov.* TYPE: MEXICO. Baja California Norte: Cañon 10 mi N of San Vicente, near Mpio. Ensenada, 3 May 1969, *D. Wilken & W. Werner 7432* (HOLOTYPE: UC!).

Differt a *Erigeronte breweri* A. Gray var. *covillei* (E. Greene) Nesom caulibus ac phyllariis scabridiusculis.

Northwestern Baja California Norte, México (not mapped); chaparral, desert scrub, ca. 150-300 m; May-Jul.

Additional collections examined: MEXICO. Baja California Norte: Guadalupe, 2 Jun 1893, *Brandegee s.n.* (UC); ca. 7 mi N of Santo Tomás along road to Ensenada, 29 Jun 1962, *Wiggins & Thomas 415* (DS).

These plants are similar to those of var. *covillei*, but the hairs of the stems and phyllaries are extremely short, barely longer than broad, and they are long disjunct (ca. 120 miles) from the southernmost populations of var. *covillei* in Riverside Co., California.

e. *Erigeron breweri* A. Gray var. *jacinteus* (H.M. Hall) Cronq., Brittonia 6:284. 1947. BASIONYM: *Erigeron jacinteus* H.M. Hall, Univ. Calif. Publ. Bot. 1:127. 1902. TYPE: UNITED STATES. California: Riverside Co., San Jacinto Mountains, rocky ridges and peaks near Tauquitz, 8826 ft, Jun 1901, *H.M. Hall 2322* (HOLOTYPE: UC!; Isotype: JEPS).

California endemic, San Jacinto, San Bernardino, and San Gabriel, Mts. (Map 4); open, rocky crests and slopes, 2680-2900 m; Jun-Sep.

Var. *jacinteus* is recognized by the dense vestiture of the stems and leaves, very small leaves, and short, nearly prostrate stems. It is very similar to var. *breweri*, but in the San Bernardino Mountains, where they both occur, var. *jacinteus* occurs at higher elevations (var. *breweri* is found at 1210-2580 meters). In a sense, var. *jacinteus* is related to the rest of *E. breweri* as *E. miser* A. Gray is to *E. petrophilus*; further study might show that var. *jacinteus* is distinct as a species and deserves coordinate taxonomic rank with *E. breweri*.

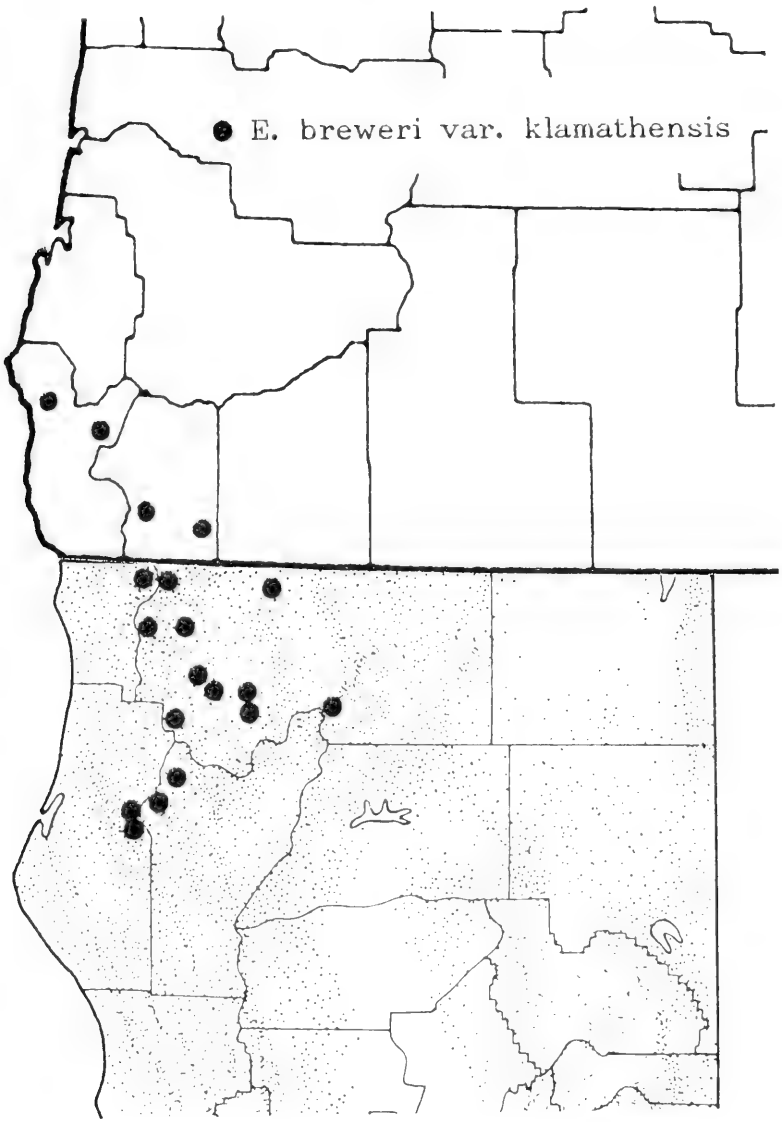
Five varieties of *Erigeron breweri* occur in the San Bernardino Mountains. These taxa appear to be altitudinally segregated, from highest to lowest as follows: var. *jacinteus*, var. *breweri*, var. *porphyreticus*, and var. *covillei* and var. *bisanctus* the lowermost, which occur at roughly similar elevations.

f. **Erigeron breweri** A. Gray var. **klamathensis** Nesom, *var. nov.* TYPE: UNITED STATES. California: Humboldt Co., Trinity Summit, 2 mi SE of Devil's Hole, exposed rocky points in woods, westerly exposure, 26 Jul 1935, *J.P. Tracy 15515* (HOLOTYPE: UC!; Isotypes: JEPS!,MO!,TEX!).

Differt a *Erigeronte folioso* Nutt. var. *confini* (Howell) Jeps. trichomatibus patentibus caulium ac foliorum, et foliis oblanceolatis brevioribusque. Differt a *Erigeronte breweri* A. Gray var. *breweri* radice lignea, trichomatibus longioribus, et phyllariis sine apicibus viridis.

California, primarily Klamath Ranges in Siskyou, Trinity, and Shasta cos., adjacent Oregon in Curry and Josephine cos. (Map 5); open, rocky slopes, rock crevices, 1580-2140 m; Jun-Sep.

Additional collections examined: UNITED STATES. California: Del Norte-Siskyou Co. line, Little Grayback, 14 Aug 1934, *Lee 1109* (UC). Humboldt Co.: Trinity Summit, 25 Sep 1919, *Tracy 5299* (UC); Trinity Summit at Water Dog Lakes, 26 Jul 1935, *Tracy 14271* (UC); Trinity Summit, Devil's Hole, 17 Jul 1932, *Tracy 10696* (UC). Siskyou Co.: top of grade between Sawyer's Bar and Etna, 8 Sep 1948, *Alexander & Kellogg 5002* (UC); slopes SE of White Mt., 1 Jul 1961, *Dempster 1832* (UC); Baldy Mt., 13 Jul 1950, *Hoffman 3552* (UC); Marble Mts., Elk Mt., 6 Aug 1939, *Howell 15101* (CAS,LL); Devil's Backbone, 17 Jul 1902, *Jepson 2071* (JEPS), 22 Jul 1902, *Jepson 2101*



Map 5. *Erigeron breweri* var. *klamathensis*.

(JEPS); trail from English Lake to Hancock Lake toward Marble Mt., 19 Aug 1928, *Kildale 6527* (DS); at Del Norte Co. line, Little Grayback, 14 Aug 1934, *Lee 1109* (DS); Mt. Eddy, near Shasta, Jul 1880, *Lemmon s.n.* (UC); Salmon Mts., high lake basins, vicinity of English Peak, 19 Aug 1968, *Oettinger 588* (UC). Trinity Co.: Trinity Summit, near Ranger Station, 24 Jul 1935, *Tracy 14204* (DS,JEPS,MO,UC); Siskyou Mts., Rock Gulch off Jaynes Canyon, 6 Aug 1934, *Wheeler 3055* (DS-2 sheets, UCR). Oregon. Curry Co.: banks of Rogue River at Brushy Bar, 27 Apr 1947, *Baker 3819* (UC); Rocky Peak, 12 mi SE of Port Orford, 25 Jul 1919, *Peck 8932* (MO). Josephine Co.: Mt. Grayback, Siskyou Mts., 2 Aug 1935, *Tracy 12460* (MO); Baby Foot Lake area near Cave Junction, 23 Jul 1980, *Vale s.n.* (CAS).

These plants form the northernmost segment of the range of *Erigeron breweri*. Cronquist (1947) included a Lemmon collection of var. *klamathensis* (Shasta Co.: Lassen's Peak, 1870's, *Lemmon s.n.* [JEPS,UC]) in var. *breweri*, but he did not recognize *E. breweri* from any localities further north. It is likely that the label of these plants was interchanged with a collection by Lemmon (of typical var. *breweri*, said on the label to be from Mt. Eddy, but far out of range for that taxon).

Var. *klamathensis* is similar to var. *breweri* in its merely glandular phyllaries but more like var. *porphyreticus* in its strongly woody bases. The relatively sparse, stiffly hirsute vestiture of long hairs in var. *klamathensis* is not encountered in any of the other varieties of the species. Many collections of var. *klamathensis* have been identified previously as *E. foliosus* var. *confinis*, which usually is nearly glabrous to sparsely strigose and produces longer, linear leaves. Some plants of the two taxa, however, are very similar in habit, and they may prove to be closely related (see additional comments following var. *confinis*).

g. *Erigeron breweri* A. Gray var. *porphyreticus* (M.E. Jones) Cronq., Brittonia 6:283. 1947. BASIONYM: *Erigeron porphyreticus* M.E. Jones, Contr. West. Bot. 8:33. 1898. TYPE: UNITED STATES. Nevada: Mineral Co., Hawthorne, Big Indian Canyon, 27 May 1897, *M.E. Jones s.n.* (HOLOTYPE: POM; Isotypes: MO,US!). *Erigeron foliosus* Nutt. var. *porphyreticus* (M.E. Jones) Compton, Bull. So. Calif. Acad. Sci. 33:53. 1934.

Erigeron petrocallis E. Greene, Erythea 3:21. 1895. LECTOTYPE (designated here): UNITED STATES. Nevada: Humboldt Co., West Humboldt Mountains, Jul 1894, *E.L. Greene s.n.* (ND-G!). A different collection by Greene has been annotated by previous workers as type material, but the specimen cited here is the only one that agrees with the protologue.

Chromosome number, n=9 (Montgomery & Yang 1960, the voucher apparently cultivated from "Rancho Santa Ana").

Western half of Nevada to the eastern edge of the Sierra Nevada in California, Mono Co. south into the Mojave Desert (Map 3); open, rocky sites in sagebrush to ponderosa pine, (1220-)1520-2530 m; May-Aug(-Sep).

Duplicates of a collection of typical *Erigeron breweri* var. *porphyreticus* were distributed and identified by Munz with the varietal name "*roosii*;" the specimens were marked as types, but the name apparently was never published.

Var. *porphyreticus* is similar to var. *breweri* in the production of slender, rhizomatous branches, spreading-deflexed stem vestiture, and blue ligules; it differs in its wirier stems, generally greater development of flowering branches, larger heads, and hirsute-hispid phyllaries with broad stramineous-indurated margins, lacking green, *Aster*-like tips. For the most part, the ranges of the two taxa are separate (Maps 3 and 4), but they are sympatric in Mono Co. and northern Inyo Co. and adjacent Nevada, as well as in the San Bernardino Mountains, and they appear to intergrade at least in Mono and Inyo cos. In the Kingston Range of San Bernardino Co., where numerous collections of *Erigeron breweri* have been made, most of the plants can be referred to var. *porphyreticus*, as identified here, but some have smaller heads and have relatively few nonglandular hairs. Were these not in populations of other typical var. *porphyreticus*, they would be best identified as var. *breweri*.

Some of the plants included here with var. *porphyreticus* (cited below) from San Bernardino Co. were identified by Cronquist (1947) as var. *covillei*. Var. *porphyreticus* in this southwestern portion of this county occurs at 1220-2440 meters elevation, higher for the most part than var. *covillei*.

Specimens of var. *porphyreticus* examined from southwestern San Bernardino Co.: San Bernardino Mts.: Bear Valley, 5 Aug 1902, *Abrams 2886* (UC), Jul 1909, *Davidson 2169* (JEPS); Bear Lake, 8 Jul 1931, *Clokey 5317* (UC); San Gorgonio Wilderness Area, Lower South Fork Meadow, 15 Aug 1976, *Davidson & Thorne 4716* (UC); Hesperia, 14 Jun 1895, *Parish 3603* (JEPS,UC-2 sheets).

6. *Erigeron elmeri* (E. Greene) E. Greene

Erigeron elmeri (E. Greene) E. Greene, *Fl. Franc.*, part IV, p. 393. 1897. BASIONYM: *Aster elmeri* E. Greene, Pittonia 2:170. 1891. LECTOTYPE (Cronquist 1947): UNITED STATES. California: Tuolumne Co., Grand Canyon of the Tuolumne River, summer [1891, as on the label], *V. Chesnut & E. Drew s.n.* (ND-G!). *Erigeron breweri* A. Gray var. *elmeri* (E. Greene) Cronq., Brittonia 6:284. 1947. The protologue notes that the type collection was made in "summer 1890," but I have seen no other specimen that might be the one referred to by Greene, nor is

there any other such in ND-G (*fide* B. Hellenthal). Both the protologue and collection label note that the specimen was collected in the "Grand Canyon of the Tuolumne" by Chesnut & Drew, the only difference being that of one year in date. Although it is not annotated in any way, this is evidently the specimen that Cronquist (1947) referred to as the type, and his choice is accepted here. It seems most likely that either the label or the publication of *Aster elmeri* was inadvertently supplied with the wrong date.

Stems prostrate-ascending to nearly erect, 6-20 cm long, from slender, woody rhizomes or rhizomelike caudex branches. Stems and leaves eglandular, sparsely to moderately strigose with thin-based, closely appressed to ascending-appressed hairs. Leaves narrowly oblanceolate or oblong, 5-20 mm long, 1-2 mm wide. Heads 7-10 mm wide; phyllaries minutely glandular, without other vestiture, inner phyllaries 3.5-5.0 mm long, often purple-tipped. Ray flowers 12-21, the corollas 6-9 mm long, drying bluish. Disc corollas 3.5-4.0 mm long. Achenes 1.6-2.5 mm long; pappus bristles 18-26.

California endemic, central High Sierra Nevada (Map 1); ledges, crevices, cracks, talus, 1300-3300 m; Jun-Sep.

Erigeron elmeri is distinguished by its low habit with wiry, trailing to ascending stems, very small leaves, sparsely strigose vestiture, small heads, and pink to lavender ligules. It has been treated as a variety of *E. breweri* because of putative intergradation between the two, but the occurrence of intermediates has not been confirmed in the present study. In contrast, among the 30 separate collections of *E. elmeri* examined, only a single one has stem vestiture that might be considered to approach that of *E. breweri* (Lake Tenaya, Yosemite, *Eastwood 462*-UC). On some branches of this collection, the stem hairs are ascending-appressed; on others, there is a mixture of spreading and ascending hairs. This atypical variation may reflect an influx of genes from *E. breweri*, but the two taxa are sympatric and, with the possible exception of a few plants, they retain their integrity, providing convincing evidence of genetic isolation. A specimen cited by Cronquist as var. *elmeri* from Tulare Co. (*Hall & Babcock 5697*-UC), which has spreading stem pubescence, also is stipitate-glandular and clearly is a collection of *E. aequifolius*.

7. *Erigeron foliosus* Nutt.

Erigeron foliosus Nutt., Trans. Amer. Philos. Soc. 2, 7:309. 1840. TYPE: UNITED STATES. California: Santa Barbara Co., near Santa Barbara, [1836], *T. Nuttall s.n.* (Possible isotype: PH *fide* Cronquist 1947).

Stems 20-100 cm long, often arising from thin, rhizomelike or caudexlike branches, erect but commonly basally ascending, branched near the apex;

stems, leaves and phyllaries glabrate to sparsely invested with appressed hairs. Leaves linear to oblanceolate, entire, 10-65 mm long, 1-5(-10) mm wide. Heads 10-16 mm wide, in a loose terminal cluster, rarely solitary; phyllaries glabrous to moderately hairy, sometimes glandular. Ray flowers 15-60, the corollas 5-15 mm long, usually blue. Disc corollas 3.5-5.5 mm long. Achenes (1.8-)2.4-3.0 mm long; pappus bristles 20-34.

In the present treatment, *Erigeron foliosus* is distinguished from the other taxonomically complex, radiate species of the section, *E. breweri*, by its glabrate to sparsely strigose stems, as contrasted with the densely hispidulous stems of the latter. It is perhaps an oversimplified hypothesis, but the radiate *E. elmeri* and *E. oxyphyllus* are similar to *E. foliosus* in stem vestiture and may be most closely related to it.

The varieties of *Erigeron foliosus* are separated primarily by relatively small differences in vestiture. For the most part, the taxa are represented by a series of essentially allopatric population systems (Maps 6 and 7). Var. *mendocinus* (E. Greene) Nesom and var. *confinis* as well as var. *foliosus* and var. *franciscensis* have slightly overlapping or at least parapatric distributions and form intermediates in the areas where they meet.

Key to the varieties of *E. foliosus*

1. Phyllaries densely and prominently glandular, 0.8-1.0 mm wide, the margins usually with a broad scarious rim. .....(3)

1. Phyllaries eglandular or sparsely and obscurely glandular, 0.5-0.8 mm wide, the margins usually thick or with only a narrow scarious rim. (2)

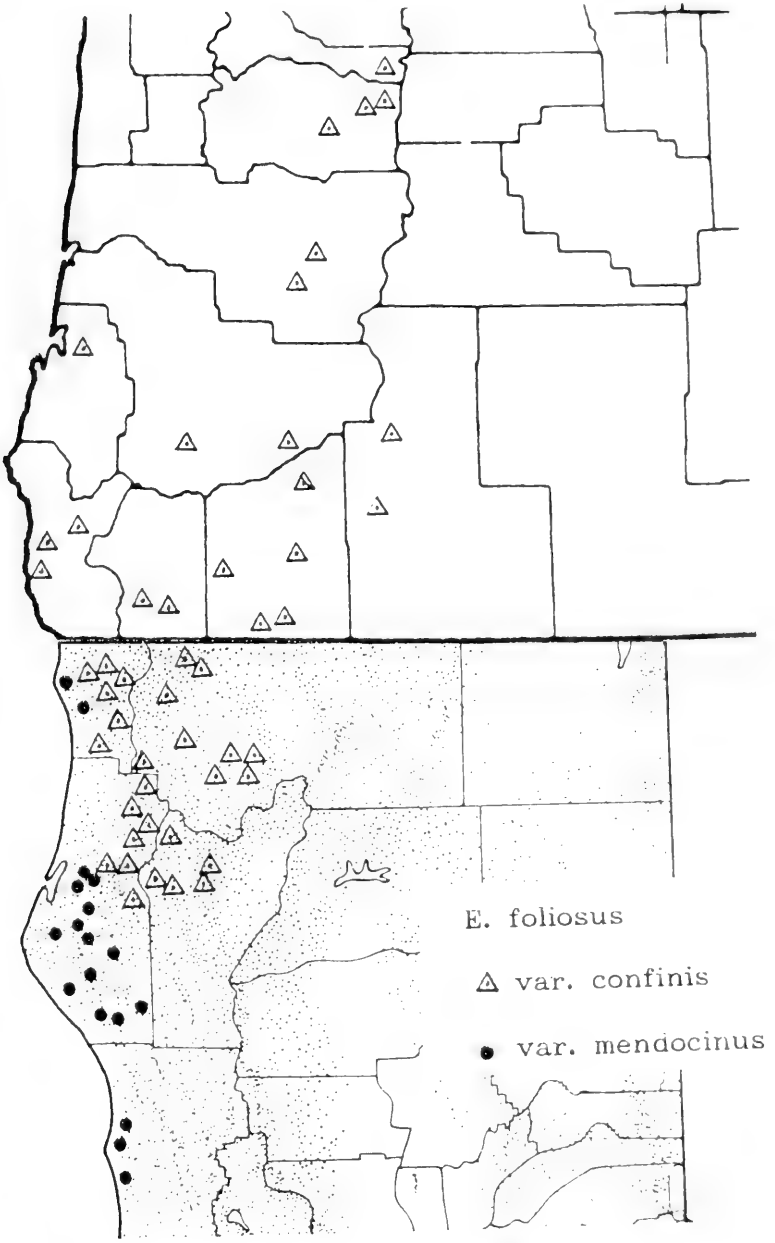
   2. Leaves (3-)4-6 cm long usually with acute apices, often mostly oriented in one direction to one side of the stem; inner phyllaries (4.0-)5.0-6.0 mm long. ..... var. *hartwegii*

   2. Leaves 2-4(-5) cm long usually with rounded apices, without a prominent unidirectional orientation; inner phyllaries 3.2-4.5 mm long. ..... var. *foliosus*

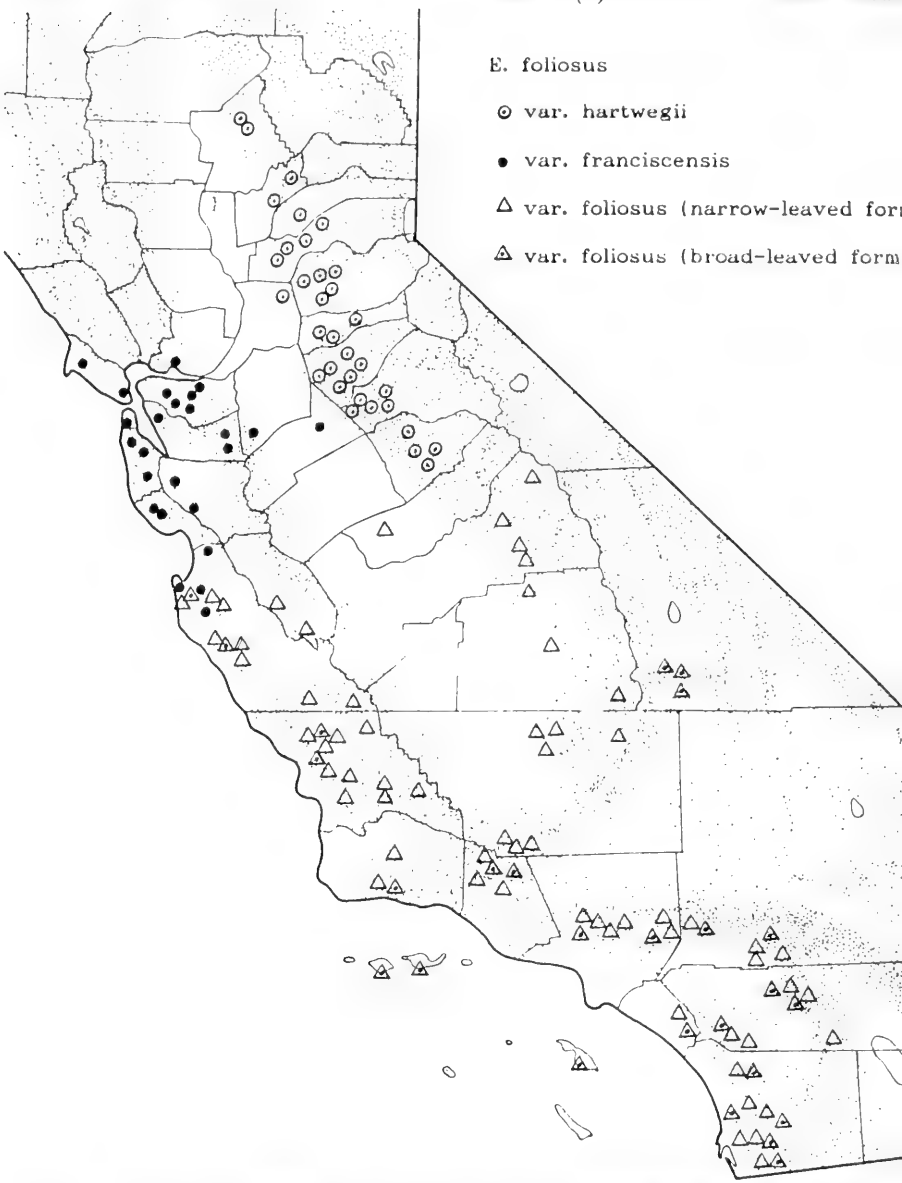
3. Phyllaries without eglandular hairs; leaves mostly 1-2 mm wide. ..... var. *confinis*

3. Phyllaries moderately to densely strigose-hirsute; leaves mostly 2-4 mm wide. .....(4)

   4. Leaf lamina sparsely to moderately strigose; phyllaries with a prominent, raised, orange resinous midvein; ray corollas 7-10 mm long. ..... var. *franciscensis*



Map 6. *Erigeron foliosus* (var. *mendocinus* and var. *confinis*).



Map 7. *Erigeron foliosus* (var. *foliosus*, var. *hartwegii*, and var. *franciscensis*). For var. *foliosus*, the broad leaved forms and narrow leaved forms are mapped separately to show their nearly complete sympatry; many of the symbols were assigned arbitrarily where intermediates in leaf width were involved. The range of var. *foliosus* extends into northwestern Baja California Norte.

4. Leaf lamina glabrous or glabrate, margins and midvein ascending ciliate; phyllaries usually without a distinct, orange resinous midvein; ray corollas 10-15 mm long. ..... var. *mendocinus*

a. *Erigeron foliosus* Nutt. var. *confinis* (Howell) Jeps., *Man. Fl. Pl. Calif.* 1056. 1925. BASIONYM: *Erigeron confinis* Howell, Erythea 3:35. 1895. LECTOTYPE (designated here): UNITED STATES. Oregon: Josephine Co., Siskyou Mts., near Waldo, Jul 1887, *T.J. Howell 1507* (WS; Isolectotypes: MO!,MI,NY,UC!,US!). The protologue says "On high rocky ridges of the S. Mts., July 1886" but specimens matching the locality description are "1887." The sheets so cited (Cronquist marked the MO and UC sheets as "isotype") were distributed by Howell with the unpublished epithet "siskyouensis."

Inner phyllaries 4.0-5.0 mm long. Ray corollas 9-12 mm long. Disc corollas 3.5-5.0 mm long.

Klamath Ranges of California and adjacent southwestern Oregon (Map 6); rocky sites, chaparral to fir woods, over a variety of soils but often on serpentine, (rarely to 15-)(150-)750-2000(-2200) m; May-Aug.

Plants of *Erigeron foliosus* var. *confinis* typically are low (1-2 dm tall), linear leaved, and have densely glandular phyllaries without other vestiture. There are apparent intermediates with var. *mendocinus* where their ranges meet, particularly in the region of the Smith River in Del Norte Co. and the Klamath River in Humboldt Co. Some plants identified as var. *confinis* are very similar in habit to *E. breweri* var. *klamathensis* (particularly in Siskyou and Trinity cos., e.g., *Tracy 19196*-UC), and the possibility of gene flow or very recent common ancestry between them should be investigated. The two taxa are sympatric over a considerable part of their ranges (Maps 5 and 6).

b. *Erigeron foliosus* Nutt. var. *foliosus*

Erigeron stenophyllus Nutt., J. Acad. Nat. Sci. Philad. 2, 1 (Pl. Gamb.): 176. 1847. TYPE: UNITED STATES. California: Monterey Co., near Monterey, [1842], *W. Gambel s.n.* (Probable isotype: GH!); not Hook. & Arn. 1836; not A. Gray 1857; not D.C. Eaton 1871. *Erigeron foliosus* Nutt. var. *stenophyllus* (Nutt.) A. Gray, *Bot. Calif.* 330. 1876. *Erigeron nuttallii* Heller, *nom. nov.* Bull. Torrey Bot. Club 25:628. 1898.

Diplopappus occidentalis Hook. & Arn., *Bot. Beechey's Voy.*, Suppl. 350. 1839. TYPE: UNITED STATES. California: [ca. 1830], *D. Douglas s.n.* (not seen). *Erigeron douglasii* Torr. & Gray, *nom.*

nov., *Fl. N. Amer.* 2:177. 1841. Not *Erigeron occidentalis* Nutt., 1840. Torrey & Gray were unaware that *Erigeron foliosus* Nutt., the earliest available name for this species but which they treated as a "Species unknown to us," was the same as *Diplopappus occidentalis*. They indicated that they had seen the original specimen collected by Douglas. The identity of *E. occidentalis* Nutt. has not been ascertained, but with "very numerous, red" rays and "subserrulate" leaves, it clearly is not part of the *E. foliosus* group. Based on the description, albeit relatively generalized, and the information regarding the collecting localities of Douglas (Jepson 1933), it seems clear that the plants of his collection are *E. foliosus* var. *foliosus*, in the sense of the present study. Gray (*Synopt. Fl. N. Amer.* 1[2]:215. 1884) recognized the synonymy of *E. douglasii* with *E. foliosus*.

Erigeron foliosus Nutt. var. *tenuissimus* A. Gray, *Synopt. Fl. N. Amer.* 1(2):215. 1884. LECTOTYPE (designated here): MEXICO. Baja California Norte. Hanson's Ranch, 30 Jul 1883, *C.R. Orcutt 1000* (GH!; Isolectotype: UC!). In the original description, Gray's citation was "San Diego Co., on the Mexican border and within lower California, *Parry, Palmer, Orcutt.*"

Erigeron tenuissimus E. Greene, Pittonia 3:25. 1896. LECTOTYPE (designated here): UNITED STATES. California: Ventura Co., near Ventura, Jun 1893, *Miss A. Symes s.n.* (ND-G!; Isolectotype: UC, as cited by Cronquist, but not located in the present study).

Erigeron striatus E. Greene, Bull. So. Calif. Acad. Sci. 1:39. 1902. LECTOTYPE (designated here): UNITED STATES. California: San Bernardino Co., Huston Flat, Transition Zone of the San Bernardino Mts., Aug 1900, *W.R. Shaw 36* (ND-G!; Isolectotype: DS!).

Erigeron setchellii Jeps., *Fl. W. Mid. Calif.* (ed. 1) 568. 1901. LECTOTYPE (designated here): UNITED STATES. California: [San Joaquin Co.], "arid plains of the Lower San Joaquin" [somewhere between Mossdale (near present day Manteca) and Oakdale], 27 Jun 1896, *W.A. Setchell & W.L. Jepson s.n.* (JEPS!; Isolectotype: JEPS!). Locality information from Jepson's field notebook was supplied by Mrs. A.Q. Howard.

Erigeron fragilis E. Greene, Bull. So. Calif. Acad. Sci. 1:39. 1902. LECTOTYPE (designated here): UNITED STATES. California: Orange Co., Trabuco Canyon, 16 Jun 1901, *L. Abrams 1801* (ND-G!; Isolectotype: DS!).

Erigeron foliosus Nutt. forma *grinnellii* Cronq., Brittonia 6:279. 1947. TYPE: UNITED STATES. California: Los Angeles Co., Mt. Wilson, 4 Jul 1904, *F. Grinnell s.n.* (HOLOTYPE: CAS!).

Inner phyllaries 3.2-4.5 mm long. Ray flowers 15-49, 6-10 mm long. Disc corollas 3.5-4.0(-5.0) mm long. Chromosome number, n=9 (Semple 1985; Strother 1972; Solbrig *et al.* 1964; Raven *et al.* 1960).

California, widespread in the southwestern part of the state, adjacent Baja California Norte, México (Map 7); dry, open, rocky or grassy slopes, chaparral, oak to pine or pine-fir woodlands, (40-)300-2250(-2900) m; May-Aug(-Sep).

Plants of *Erigeron foliosus* with linear leaves (var. *stenophyllus*) have traditionally been separated from those with much broader, oblanceolate leaves (var. *foliosus*), but when confronted with a large number of specimens, the correspondingly large number of intermediates and the nearly exact congruence of the geographic ranges of the two putative varieties makes it impossible to separate them in an unarbitrary taxonomy. In the view here, var. *foliosus* comprises a series of plants with leaves varying from filiform to oblanceolate and broadly oblanceolate (the latter in extreme form in forma *grinnellii*).

The habit of *Erigeron foliosus* var. *foliosus* is somewhat variable, but it is most commonly similar to that of *E. breweri* var. *covillei*, with stems basally ascending and gradually thickened towards the base. Complete root systems have been collected only rarely. Some plants identified here as var. *foliosus*, particularly in Tulare and Kern counties (*e.g.*, S. Fork King's River, *Jepson 773A*-JEPS), have stems densely invested with minute, slightly spreading-ascending hairs and phyllaries densely glandular. These may have originated as hybrids between var. *foliosus* and *Erigeron breweri*. See other comments following var. *franciscensis* regarding variability in var. *foliosus*.

c. **Erigeron foliosus** Nutt. var. **franciscensis** Nesom, *var. nov.* TYPE: UNITED STATES. California: San Mateo Co., Lake Merced, Jun 1908, *K. Brandegee s.n.* (HOLOTYPE: UC!).

A *Erigeronte folioso* Nutt. var. *folioso* phyllariis longioribus glandulosis sed trichomatibus non glandulosis densioribus.

Inner phyllaries (4.0-)5.0-6.0 mm long. Ray flowers 28-48, 7-10 mm long. Disc corollas 4.5-5.0 mm long.

California endemic, primarily the San Francisco Bay Area (Map 7); grassy dunes, chaparral, oak woodlands, 2-800 m; May-Oct.

Representative collections examined: UNITED STATES. California: Alameda Co.: Oakland, 9 Jul 1881, *Jones 2374* (CAS,DS); 25 mi N of Cedar Mts, 13 Oct 1929, *Mason 5511* (UC). Contra Costa Co.: Mount Diablo, Inner Black Hills E of the meridian, 5 Sep 1932, *Bowerman 1550* (UC); hills between Antioch and Marsh Creek, 16 Jan 1907, *K. Brandegee s.n.* (UC); Walnut Creek, 20 Jun 1892, *Greene s.n.* (UC). Marin Co.: San Francisco, Jul 1908, *K. Brandegee s.n.* (UC-2 sheets); near Chinese Camp, 25 Jun 1944,

Howell 19663 (CAS,UC); Tiburon Peninsula, Paradise Drive, 2.4 mi NW of road to Naval Net Depot, 29 Jun 1961, *Penalosa 1871* (CAS,UC). Monterey Co., Pajaro Hills, Jun-Jul 1899, *Chandler 437* (UC); Pt. Lobos, 6 Aug 1912, *Eastwood 1568* (CAS); mt. above Carmel Valley, 7 Jul 1962, *Howitt 1974* (CAS). San Joaquin Co., Lower San Joaquin River, 27 Jun 1896, *Jepson s.n.* (JEPS). San Mateo Co.: N end of Sawyer Ridge, San Francisco Watershed Reserve, 23 Jul 1983, *Buck 448* (UC); Belmont, 17 Jun 1893, *Davy 804* (UC); near Searsville Dam, 14 Jun 1895, *Dudley s.n.* (DS); E-W canyon draining into Lake Merced, just N of the San Francisco Golf and Country Club golf course, 17 Jul 1950, *Raven 2608* (CAS,UC). Santa Clara Co.: Saratoga, Sep 1893, *Davy 829* (UC); Black Mountain, Jul 1903, *Elmer 4589* (CAS,DS,MO,UC). Santa Cruz Co.: Bear Creek Canyon, ca. 4 mi from Boulder Creek, 6 Aug 1953, *Hesse 1178* (JEPS); Empire Grade, Ben Lomond Mt., 15 Jul 1953, *Thomas 3478* (DS,JEPS). Solano Co., S end of basalt hill at Thomasson, 16 Jun 1937, *Jepson 18415* (JEPS). Stanislaus Co., Oakdale, 30 Jun 1896, *Jepson s.n.* (JEPS).

Var. *franciscensis* is closely similar to var. *foliosus*, but for the most part the two taxa are geographically well separated. A few collections that technically would be identified as var. *franciscensis* are well within the range of var. *foliosus* (e.g., Los Angeles Co., Leona, *Michener & Bioletti s.n.*-UC; San Luis Obispo Co., Paso Robles country, *Blochman s.n.*-UC); other scattered collections identified and mapped as var. *foliosus* have densely glandular phyllaries, but the phyllaries are shorter (3.2-4.5 mm long vs. [4.0-]5.0-6.0 mm long in var. *franciscensis*), generally more sparsely invested with non glandular hairs, without prominently scarious margins, and the plants appear to be closely linked to the variability in others of more typical morphology. The two varieties appear to be sympatric in northern Monterey County, and intermediates occur there.

In both var. *foliosus* and var. *franciscensis*, the midvein of each phyllary is prominently raised and orange-resinous, but the midvein is low and barely discernible as orange in var. *mendocinus*; in var. *hartwegii* and var. *confinis* it is more variable, sometimes prominently orange, but often not.

d. *Erigeron foliosus* Nutt. var. *hartwegii* (E. Greene) Jeps., *Man. Fl. Pl. Calif.* 1056. 1925. BASIONYM: *Erigeron hartwegii* E. Greene, Erythea 3:21. 1895. LECTOTYPE (Cronquist 1947): UNITED STATES. California: Locality and date unspecified, *K.T. Hartweg 350* (NY!; Isolectotype: GH!). In the original description, Greene noted that this taxon had been "first collected by Hartweg, afterwards by Fremont, Bigelow, and by the present writer." Bentham (*Pl. Hartweg.* 316. 1849.) earlier had identified this same collection as *E. decumbens* Nutt. The notation "*Hartweg 1774*" denotes the number of sequential listing in *Plantae*

Hartwegianae rather than the collection number.

Erigeron blasdalei E. Greene, Erythea 3:124. 1895. LECTOTYPE (designated here): UNITED STATES. California: Calaveras Co., dry rocky soil, Stanislaus River near McCormic's Bridge, 10 Jun 1895, *W.C. Blasdale s.n.* (UC!; Probable isolectotype: ND-G!). The latter specimen is marked only as "*Erigeron blasdalei*," but the plants match those on the UC sheet.

Inner phyllaries (4-)5-6 mm long. Ray flowers 26-50, 8-13 mm long. Disc corollas 4.0-5.5 mm long.

California endemic, north and central Sierra Nevada Foothills (Map 7); rocky sites, commonly along rivers, hills in oak or pine-oak woodlands, 100-600 m; Apr-Jul.

Var. *hartwegii* has a geographically discrete distribution and the plants are very constant in morphology. Further comments are given following *Erigeron mariposanus* Congdon.

e. **Erigeron foliosus** Nutt. var. **mendocinus** (E. Greene) Nesom, *comb. et stat. nov.* BASIONYM: *Erigeron mendocinus* E. Greene, Leafl. Bot. Obs. Crit. 2:9. 1909. LECTOTYPE (designated here): UNITED STATES. California: Mendocino Co., Big River, Jul 1903, *J. McMurphy 353* (CAS!). Only a single collection was noted in the protologue, but its place of deposition was not specified.

Inner phyllaries 5.0-6.5 mm long. Ray flowers 25-48, 10-15 mm long. Disc corollas 3.8-5.0 mm long.

California endemic, North Coast Ranges (Map 6); bars, banks, and ledges along rivers, dry slopes, 30-750 m; May-Aug.

Representative collections examined: UNITED STATES. California: Del Norte Co.: Smith River near Myrtle Creek, 24 Jun 1938, *Parks & Tracy 11458* (UC); Smith River near Van Deventer Ranch, 29 Jun 1938, *Van Deventer 127* (JEPS). Humboldt Co.: Van Duzen River, mouth of Grizzly Creek, 11 Jul 1916, *Abrams 6055* (DS,LL,UC); Mad River, 10 Jul 1888, *Chesnut & Drew s.n.* (UC); South Fork Eel River, Upper Look Prairie, 29 May 1934, *Constance 720* (JEPS); near Alder Point, 22 Jun 1937, *Eastwood & Howell 4731* (CAS); Junction, E of Arcata, 16 Jul 1931, *Jones 29149* (MO,UC); near Ettersburg, 25 Jun 1927, *Kildale 3585* (DS); Bridgeville, 23 Jul 1928, *Kildale 5694* (DS); near Hydesville, bluffs along Van Duzen River, 2 Aug 1901, *Tracy 1241* (UC); Grasshopper Ridge, head of Canoe Creek, 4 Sep 1916, *Tracy 4756* (UC); Mad River gravel bar at Essex, 11 Jun 1924, *Tracy 6695* (UC); Bull Creek to Mattole Road, near ridge summit, 4 Jul 1930, *Tracy 8829* (DS,JEPS,LL,UC); Trinity River near Willow Creek, 17 May 1931, *Tracy 9433* (UC); Garberville, 18 Jul

1942, *Tracy 17284* (UC); Blue Slide on Van Duzen River, 24 Jul 1951, *Tracy 19625* (UC). Mendocino Co.: near Mendocino, May 1898, *Brown 786* (MO); Fort Bragg, 1914, *Mathews s.n.* (JEPS); Fort Bragg, 8 Jul 1933, *Stahelin s.n.* (UC).

These plants have been previously identified, for the most part, as *Erigeron foliosus* var. *hartwegii*, but the two are geographically and morphologically distinct.

8. *Erigeron inornatus* (A. Gray) A. Gray

Erigeron inornatus (A. Gray) A. Gray, Proc. Amer. Acad. Arts 16:88. 1881. BASIONYM: *Erigeron foliosus* Nutt. var. *inornatus* A. Gray, *Bot. Calif.* 1:330. 1876. LECTOTYPE (Cronquist 1947): UNITED STATES. California: Mendocino Co., Eel River, hot, sunny slopes, 1868-69, *A. Kellogg & Harford 347* (GH!; Isolectotypes: MO!,NY,US!).

Stems 2-7(-9) dm long, branched near the apex, basally decumbent but quickly erect, arising from a woody taproot, at least the upper portions glabrous. Leaves narrowly oblong-oblanceolate, (1-)2-6 cm long, 2-7 mm wide, the lamina glabrous or sparsely strigose, the lower usually with short, upcurved hairs, margins sparsely and widely ciliate with short, upturned hairs. Heads 7-12 mm wide, 5-many in a terminal, flat topped cluster; phyllaries glabrous, rarely minutely glandular, with broad, stramineous lateral areas and a thin, orange midvein, the inner 4.5-5.5 mm long. Ray flowers absent. Disc corollas 3.8-4.5 mm long. Achenes 2.0-3.0 mm long; pappus of 28-45(-60) bristles.

Key to the varieties of *E. inornatus*

1. Upper stems densely hirsutulous with slightly deflexed hairs, sometimes densely invested with strigose ascending hairs. ..... var. *keilii*

1. Upper stems usually sparsely strigose to glabrous. ..... (2)

   2. Stems 10-20 cm long, decumbent-ascending, with spreading-deflexed hairs below the middle, appressed above the middle; middle and lower leaves with hispid lamina and margins with stiff, spreading cilia; inner phyllaries 5.0-6.5 mm long. ..... var. *calidipetris*

   2. Stems 30-70(-90) cm long, basally ascending, the upper portions erect, with appressed hairs below the middle; middle and lower leaves with short strigose lamina and eciliate margins; inner phyllaries 4.5-5.5 mm long. ..... var. *inornatus*

a. *Erigeron inornatus* (A. Gray) A. Gray var. *inornatus*

Erigeron douglasii Torr. & Gray var. *eradiatus* A. Gray, *Pac. R.R. Rep.* 12(2):52. 1860. TYPE: UNITED STATES. Washington. [Yakima Co.,] sandy pine forest on the tableland east of Mount Adams, *J.G. Cooper s.n.* (not seen). *Erigeron eradiatus* (A. Gray) Piper, Contr. U.S. Natl. Herb. 11:568. 1906.

Erigeron inornatus (A. Gray) A. Gray forma *subradiatus* S.F. Blake, J. Washington Acad. Sci. 19:270. 1921. TYPE: UNITED STATES. California: Placer Co., Tahoe Tavern, 1900 m, 15 Aug 1927, *S.F. Blake 10302* (HOLOTYPE: US!; Isotypes: GH-2 sheets!,LL-2 sheets!).

Erigeron inornatus (A. Gray) A. Gray forma *pseudoradiatus* S.F. Blake, J. Washington Acad. Sci. 28:487. 1938. TYPE: UNITED STATES. Nevada: Washoe Co., public campground, Mt. Rose, 7 mi W of Reno Hot Springs, 1700 m, 12 Jul 1937, *W.A. Archer 5580* (HOLOTYPE: US!; Isotype: LL!).

Chromosome number, n=9 (Semple 1985; Strother 1983; Anderson *et al.* 1974; Raven *et al.* 1960).

Widespread in northern California (Map 2), to Oregon, southern Washington, and westcentral Nevada in Douglas, Ormsby, and Washoe cos.; chaparral to oak, pine, or pine-fir woods, (150-)750-2300 m but mostly 1050-1900 m; Jun-Sep(-Oct).

Erigeron inornatus has traditionally included varietal taxa recognized as *E. angustatus*, *E. biolettii*, *E. reductus*, and *E. petrophilus* in the present treatment. *Erigeron petrophilus* is broadly sympatric with *E. inornatus* (Maps 2 and 8), and *E. angustatus* is geographically and morphologically distinct. Some intermediates apparently are formed between *E. inornatus* and both *E. biolettii* and *E. reductus* (see the latter two for further comments).

Erigeron inornatus has the geographic widest range of all the taxa included here in sect. *Linearifolii*, and typical plants (with glabrous stems, leaves, and phyllaries) occur over its whole range. Plants with minutely glandular phyllaries, however, occur sporadically through the range and are within normal variability for the species. Some of the atypical variation in the species occurs in the sierra of eastcentral California and adjacent Nevada. As noted by Cronquist (1947), some plants there produce phyllaries and uppermost cauline surfaces that are slightly glandular as well as phyllaries and stems that are sparsely hirsutulous or minutely strigose (*e.g.*, Tuolumne Co., *Congdon s.n.*; Placer Co., *Yates 5996*; Washoe Co., *Archer 5595*). The origin of this variation is not clear, but such plants are best placed in *E. inornatus*. Further comments on these plants are given following *E. inornatus* var. *keilii*.

From the vicinity of Mt. Rose, near Reno in Washoe Co., Nevada, a collection of plants with very small ligules produced from hermaphroditic flowers

with abortive stamens has been named *Erigeron inornatus* forma *pseudoradiatus*. Cronquist (1947) regarded forma *pseudoradiatus* as a hybrid between typically radiate *E. breweri* and typically rayless *E. inornatus*, both of which also are known from the vicinity. Two other collections of more or less the same morphological form also were made at about the same time (*Archer 6401*-with longer, apparently normal rays, and *6402*) from the same area (Galena Creek), although each of these collections apparently represents a different biotype. It would be useful and interesting to reassemble (primarily from DS,RENO, and UC) a set of collections from this area (mostly near Galena Creek) and to evaluate them in more detail, in conjunction with field studies. Among these collections are numerous atypical plants that can be identified most closely as *E. breweri* var. *porphyreticus* and *E. inornatus* var. *inornatus*: *Archer 5580, 5592, 5595, 6400, 6401, 6402*, and *Lehenbauer 890*. *Erigeron inornatus* forma *subradiatus*, a similar variant, was collected in adjacent California (Placer Co.).

Erigeron inornatus occurs in the area of Donner Lake, the type locality of *E. miser*, and a plant collected from there by E.L. Greene (Aug 1883-MO) has features that suggest it may be a hybrid between *E. inornatus* and *E. miser*.

b. **Erigeron inornatus** (A. Gray) A. Gray var. **calidipetris** Nesom, *var. nov.* TYPE: UNITED STATES. California: Siskyou Co., Porcupine Lake (a small vernal depression in an indurate lava flow), T41N, R3E, Section 10, 4280 ft, moist margin of pond at high water mark, set in *Abies concolor-Pinus ponderosa* forest, 6 Aug 1987, *D.W. Taylor 9241* (HOLOTYPE: UC!).

Differt a *Erigeronte inornato* (A. Gray) A. Gray typico caulibus brevioribus decumbentibusque trichomatibus patentibus, foliis inferis laminis hispidis ac marginibus ciliatis, et phyllariis longioribus.

California endemic, Modoc Plateau and eastern margin of the Cascade Ranges, in Modoc, Siskyou, and Shasta cos., apparently disjunct to northern Butte Co. (Map 2); sandy habitats, commonly in pine or pine-oak woodlands, ca. 1100-1400 m; Jun-Aug.

Additional collections examined: UNITED STATES. California: Butte Co.: Jonesville, 6 Aug 1930, *Copeland 490* (CAS,DS,MO). Modoc Co., sandy flat in lava beds, no other data, 1893, *M.S. Baker s.n.* (JEPS). Siskyou Co.: McCloud, 21 Jun 1923, *Bethel s.n.* (CAS); Fowler Camp, McCloud River, 28 Jun 1938, *Dearing 2179* (CAS); toward Black Fox, 15 Aug 1899, *Dudley s.n.* (DS); Bigelow's, McCloud River, 25 Jul 1921, *Eastwood 10809* (CAS). Shasta Co.: 3-4 mi E of McCloud and Bartle on Hwy 89, knob cone and yellow pine association, loose sandy soil, 10 Aug 1941, *Ferris & Lorraine 10493a* (CAS,DS).

Var. *calidipetris* is different from typical *Erigeron inornatus* in vestiture and habit and has a more limited geographical range compared to the typical variety. At least in the area of McCloud, the two taxa appear to be sympatric, and the collection from Butte County is well within the range of var. *inornatus*. *Ferris & Lorraine 10493* may have been collected in Siskyou County rather than Shasta, but the label says Shasta Co. With more detailed study, var. *calidipetris* may prove to deserve rank as a species. Further comments are given following *E. petrophilus* var. *viscidulus* (A. Gray) Nesom, to which it may be closely related.

c. **Erigeron inornatus** (A. Gray) A. Gray var. **keilii** Nesom, *var. nov.* TYPE: UNITED STATES. California: Tulare Co., ca. 3.5 mi from Balch Park, Sequoia National Forest, dry slope with incense cedar and *Arctostaphylos*, 31 Jul 1950, *R.S. Ferris & L. Lorraine 12349* (HOLOTYPE: DS!; Isotypes: CAS!,UC!).

A *Erigeronte breweri* A. Gray var. *breweri* floribus radii carentibus praecipue differt; a *E. inornato* (A. Gray) A. Gray caulibus dense minute hispidulis et phyllariis dense brevistrigosis vel glandulosis differt.

California endemic, southern Sierra Nevada Foothills of Fresno and Tulare cos. (Map 2); dry, grassy slopes and meadows, areas of conifer woodlands, 1200-2200 m; Jun-Sep.

Additional collections examined: UNITED STATES. California: Fresno Co.: Sequoia Mills, 19 Jul 1892, *Brandegee s.n.* (UC); W edge of Lake Hume, 19 Jul 1961, *Breedlove 798* (DS); Bubb's Creek, S. Fork of King's River, 1-13 Jul 1899, *Eastwood s.n.* (CAS); grade to King's River Canyon from General Grant Natl. Park, 26 Jul 1942, *Ferris & Lorraine 10832* (DS); Tehipite Valley, 6-10 Jul 1900, *Hall & Chandler 486* (DS, MO); King's River Canyon, jct of Middle and S. Fork, 29 Jun 1940, *Rose 40676* (DS). Tulare Co.: NE of Springville along Bear Creek Road, Mountain Home State Forest, Methuselah Group Campground to vicinity of Dogwood Meadow, 2 Aug 1986, *Keil 19713-B* (TEX); NE of Springville along Bear Creek Road, Mountain Home State Forest, Methuselah Group Campground; montane mixed conifer forest around meadow, 25 Jul 1991, *Keil 19662* (OBI,TEX).

The collections of *Erigeron inornatus* var. *keilii* have been made from a relatively small area of Fresno and Tulare counties, near the southernmost extension of the geographic range of *E. inornatus*. Var. *keilii* is taxonomically positioned with the latter primarily because of its rayless heads, but in its dense, typically spreading stem vestiture, it is more like the plants of *E. breweri* with which it is sympatric. The rayless plants might justifiably be treated as a variety of *E. breweri* on the basis of their vestiture, but among

other taxa within sect. *Linearifolii*, the absence of ray flowers is indicative of differentiation between species.

The plants of var. *keilii* were first called to my attention by the recent collections of Dr. David Keil of California Polytechnic State University. According to Dr. Keil's collection data, the plants of *19713-B* (rayless) were collected from a mixed population with both rayless and purple rayed forms (*Keil 19713-A*, radiate; identified here as the "tall form" of *E. breweri* var. *breweri*), although most populations in the area comprised only rayless forms. Variation in the presence or absence of ray flowers was not noted in the data of the other collections of var. *keilii*.

The stem vestiture of var. *keilii* is dense and composed of minute, spreading hairs that vary from slightly deflexed to ascending. Among the specimens of var. *keilii*, the stem hairs are ascending on *Hall & Chandler 486, Ferris & Lorraine 10832*, and *Rose 40676*; the others have spreading to slightly deflexed hairs. The phyllaries are densely short strigose and eglandular on *Ferris & Lorraine 10832, Rose 40676*, and the type, while the phyllaries are glandular without other hairs on *Hall & Chandler 486, Breedlove 798, Eastwood s.n.*, and *Brandegee s.n.*

Plants with strigose, eglandular phyllaries are designated here as typical var. *keilii*, with the hypothesis that those with merely glandular, *Erigeron breweri*-like ones have acquired these features through gene flow with *E. breweri*. The *E. breweri*-like stem vestiture also supports such an hypothesis, as does the mixed population of radiate/eradiate plants noted by Keil. Additionally, plants in a collection of radiate *E. breweri* sympatric with var. *keilii* in the vicinity of Hume Lake in Fresno Co. (17 Jul 1948, *Rose 48214*-CAS) produce densely strigose-hispidulous phyllaries similar to those of var. *keilii*, suggesting that the gene flow may be reciprocal. Further north, however, where var. *inornatus* is more common and sympatric with var. *breweri*, similar hybrids have not been collected (see notes, however, following *E. inornatus* on possible hybrids from westcentral Nevada referred to by Blake as *E. inornatus* var. *pseudoradiatus*). Occasional variants of typical *E. inornatus* var. *inornatus* from further north may produce a lightly strigose vestiture on stems and phyllaries but none with hairs so dense as var. *keilii*.

9. *Erigeron mariposanus*

Erigeron mariposanus Congdon, Erythea 7:185. 1900. LECTOTYPE (designated here): UNITED STATES. California: Mariposa Co., Mariposa, 16 Jul 1899, *I.W. Congdon s.n.* (UC!; Isolectotype: DS!). Congdon cited only one collection from the single date but did not specify its place of deposition.

Stems 15-28 cm long, decumbent-ascending, sometimes branched near the

apex, sometimes arising from short (1-4 cm), thin, rhizomelike or caudexlike branches; stems, leaves, and phyllaries sparsely to moderately strigose with loosely appressed hairs, eglandular. Leaves oblanceolate, entire, (25-)30-45 mm long, (2-)5-8 mm wide, reduced in size near the heads, axillary tufts of small leaves prominent at most nodes. Heads 8-12 mm wide, solitary or 2-3 on pedicels 15-20 mm long; inner phyllaries 4.0-5.0 mm long, 0.8-1.0 mm wide, with broad, scarious, nearly winglike margins, the outer phyllaries sparsely strigose with thin based hairs, with a prominent orange resinous midvein. Ray flowers 18-22, the corollas 7-9 mm long, bluish. Disc corollas 4.0-4.5 mm long. Achenes ca. 2.0-2.4 mm long; pappus bristles 28-32.

California endemic, central Sierra Nevada Foothills in Mariposa County (Map 9); habitat unknown, ca. 600-800 m; Jun-Aug.

Additional collections examined: UNITED STATES. California: Mariposa Co., Mariposa: *Congdon s.n.* 30 Jun 1892 (UC, on sheet with 16 Jul 1900); *Congdon s.n.* 9 Aug 1892 (DS); *Congdon s.n.* 19 Jun 1900 (UC on sheet with lectotype); *Congdon s.n.* 16 Jul 1900 (UC, on sheet with 30 Jun 1892).

These are very distinctive plants represented by several collections other than the type (over eight years, all made by Congdon). All are from "Mariposa," with no other collection data, but the present city of Mariposa is located at the southernmost margin of the range of *Erigeron foliosus* var. *hartwegii*. *Erigeron mariposanus* previously has been treated as a synonym of var. *hartwegii*, but the two are extremely different in morphology, the former immediately and most easily distinguished from var. *hartwegii* as well as all other varieties of *E. foliosus* by its short stems, short, broadly oblanceolate leaves, tufts of axillary leaves produced at most nodes, and inner phyllaries with broad, scarious margins. Details of contrast between var. *hartwegii* and *E. mariposanus* are provided in the following couplet.

1. Stems 30-85 cm long, without axillary tufts of small leaves; leaves narrowly oblanceolate to linear lanceolate, 35-80 mm long, 1-2(-4) mm wide, 17-40 times longer than wide; phyllaries without prominent scarious margins; ray flowers 26-50. ..... *E. foliosus* var. *hartwegii*

1. Stems 15-20 cm long, axillary tufts of small leaves produced at most nodes; leaves oblanceolate, (25-)30-45 mm long, (2-)5-8 mm wide (at widest point), the lower and middle 5-9(-12) times longer than wide; inner phyllaries with prominent, broad, scarious margins; ray flowers 18-22. ..... *E. mariposanus*

It may be suspected that *Erigeron mariposanus* occurs in some specialized habitat and that it may now even be extinct. In any case, the formal taxonomic recognition of these plants should stimulate an attempt to relocate the population and determine its present status.

9. *Erigeron miser* A. Gray

Erigeron miser A. Gray, Proc. Amer. Acad. Arts 13:372. 1878. LECTOTYPE (designated here): UNITED STATES. California: [Placer Co.], crevices of rocks at Donner Lake, 14 Oct 1874, *E.L. Greene 466* (GH!). Gray also cited a collection from the summit of Mt. Stanford made in Sep 1877 by *Lemmon, Gray, and Hooker*; this specimen is mounted on the same sheet as *Greene 466*.

Stems decumbent-ascending to ascending-erect, 5-25 cm long, slender, woody, and caudexlike basally, arising from a woody root, the stems and leaves villous with stiff, white hairs, also minutely glandular. Leaves narrowly obovate, 7-16 mm long, 1.0-3.5 mm wide. Heads 7-12 mm wide; phyllaries densely granular-glandular, without other vestiture, the inner (3.5-)4.0-5.0 mm long. Ray flowers absent. Disc corollas 3.2-4.5 mm long. Achenes 2.0-2.5 mm long; pappus bristles 18-25(-28).

California endemic, northern High Sierra Nevada (Map 8); talus, rock crevices, 1950-2290 m; Jul-Oct.

See comments following *Erigeron petrophilus* and *E. inornatus*.

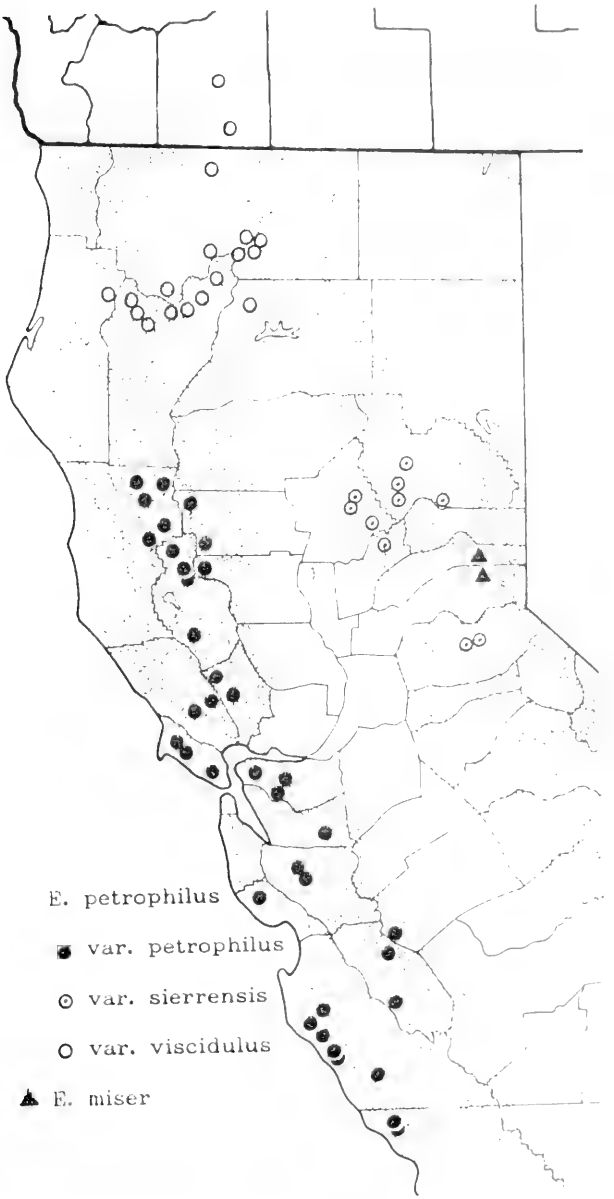
10. *Erigeron oxyphyllus* E. Greene

Erigeron oxyphyllus E. Greene, Erythea 3:20. 1895. LECTOTYPE (designated here): UNITED STATES. Arizona, Mohave Co., Yucca, May 1884, *M.E. Jones s.n.* (US!; Isolectotype: PH).

Stems shiny glabrous, 5-25 dm tall, sharply ascending basally from short, caudexlike branches, numerous, arising from a thick woody taproot. Leaves sparsely and minutely strigose, eglandular, filiform to linear oblanceolate, 0.5-1.0(-2.0) mm wide, the lower 2-5(-10) cm long, quickly reduced in length upwards, widely separated and not at all overlapping. Heads 7-12 mm wide, mostly solitary on long, bracteate peduncles, less commonly the peduncles shorter and the heads in loose clusters of 2-3; phyllaries granular-glandular, without other vestiture or the outer sometimes sparsely and minutely strigose, the inner 4-5(-6) mm long, with (1-)3 orange veins. Ray flowers 12-27(-40), the corollas 6-9 mm long, drying bluish. Disc corollas 3.0-4.0 mm long. Achenes ca. 2.0 mm long, with 2-4(-5) orange-resinous nerves; pappus bristles 17-25. Chromosome number, n=9 (Pinkava & Keil 1977).

Southern Arizona in Maricopa, Mohave, Pinal, and Yuma cos., adjacent northwestern Sonora, México (not mapped); rocky hillsides around seeps or by streams, often with *Acacia-Yucca-Coleogyne*, 700-1100 m; (Feb-)May-Jun, Oct-Nov.

This species was included by Nesom (1989) in *Erigeron* sect. *Spinosi* (Alexander) Nesom & Sundberg on the basis of its putatively close relationship with



Map 8. *Erigeron petrophilus* and *E. miser*.

E. ortegae S.F. Blake (= *Aster spinosus* Benth.). The latter species has now been segregated as the monotypic genus *Chloracantha* Nesom *et al.*, apparently more closely related to the genus *Boltonia* L'Herit. and even *Heterotheca* Cass. than to either *Erigeron* L. or *Aster* L. (Nesom *et al.* 1991). The position of *E. byei* Sundberg & Nesom, which was also included in this section, remains equivocal (Sundberg & Nesom 1990) but apparently it is not close to *E. oxyphyllus*.

Cronquist (1947) did not recognize the close relationship of *Erigeron oxyphyllus* to the *E. foliosus* group but suggested instead a relationship with *E. arenarioides* (A. Gray) Rydb. The latter, however, produces persistent basal leaves and caudex branches with densely clustered, persistent petiole bases and its ray corollas do not coil at maturity; it has been placed with one other species in *Erigeron* sect. *Arenarioides* (Rydb.) Nesom (Nesom 1989).

Among the other taxa of sect. *Linearifolii*, *Erigeron oxyphyllus* is most similar in habit and vestiture to *E. serpentinus*, but each of these probably has been independently derived from the ancestral stock that produced the widespread and variable *E. foliosus*. *Erigeron oxyphyllus* differs from all other species of the section in its cauline leaves that are sharply reduced in length upwards, and it is geographically set apart as well from the rest of the *E. foliosus* group.

11. *Erigeron petrophilus* E. Greene

Erigeron petrophilus E. Greene, Pittonia 1:218. 1888. LECTOTYPE (designated here): UNITED STATES. California: Contra Costa Co., high rocks above Wild Cat Creek, near Berkeley, Aug 1887, *E.L. Greene s.n.* (ND-G!; Isolectotype: US!). Among several collections of this species at ND-G, all identified by Greene, this sheet is the earliest one collected. It is likely that the date of "1881" cited in the protologue resulted from a typographical error for "1887." Cronquist (1947) suggested that this collection might be the type but he cited only the US sheet.

Stems decumbent-ascending, sometimes described as "sprawling," mostly 1-2 dm long, (up to 3 dm and nearly erect in Monterey Co.), from rhizome-like bases, at least the upper stems and leaves glandular (eglandular or very sparsely glandular in var. *viscidulus*, see comments below), sparsely to densely villous with loose, thin, white hairs. Leaves narrowly oblong to oblanceolate, 10-25 mm long, 1-5 mm wide, usually with long, spreading cilia along the proximal margins. Heads 8-12 mm wide, (1-)2-5(-10) in a definite corymb produced at the branch apex; phyllaries glandular, uncommonly with a few, spreading nonglandular hairs, the inner 5.5-7.0(-8.0) mm long, the apices sometimes purple, sometimes loose. Ray flowers absent. Disc corollas 4-6 mm long. Achenes (2.0-)2.5-3.0 mm long; pappus of 22-30(-35) bristles.

Erigeron petrophilus is distinguished by its ascending stems arising from distinct, fibrous rooted, rhizomelike bases, its few headed but generally compact, corymboid capitulescences, absence of ray flowers, and by its distinctive vestiture. Vars. *petrophilus* and *sierrensis* Nesom produce a densely glandular vestiture, and at least the stems are invested with loose, white, spreading, nonglandular hairs variable in density.

The observations by Cronquist (1947) regarding the distinction between *Erigeron petrophilus* and *E. miser* remain generally justifiable. *Erigeron miser* is a narrow endemic at high elevations, in contrast to the relatively wide geographic distribution at lower elevations of *E. petrophilus*. The former is distinguished morphologically primarily by its smaller heads, but there are also overlapping differences in leaf size, disc corolla length, shape of the style appendages, and the number of pappus bristles. *Erigeron miser* might also be treated as taxonomically coordinate with the three varieties of *E. petrophilus*, particularly as it terminates the eastern "arm" of the distribution of *E. petrophilus*, where it is situated as a fourth, closely related, allopatric population system (Map 8).

Key to the varieties of *E. petrophilus*

1. Stems and leaves eglandular or very obscurely glandular, the eglandular hairs mostly stiff, straight or curved. ..... var. *viscidulus*

1. Stems and leaves densely glandular, the eglandular hairs usually loose, often crinkly. ..... (2)

   2. Phyllaries with a distinctly expanded, purplish area at the apex. .. . . var. *petrophilus*

   2. Phyllary apices not purplish and differently colored from the lower portion. ..... var. *sierrensis*

a. *Erigeron petrophilus* E. Greene var. *petrophilus*

Chromosome number, $n=9$ (Strother 1983, reported as *E. miser*).

California endemic, South to North Coast Ranges, San Francisco Bay area (Map 8); rocky slopes, crevices, and talus, (530-)690-2100 m; May-Sep.

Some of the plants from the southernmost area of the range of var. *petrophilus*, particularly in Monterey and Santa Cruz counties, produce atypically tall and erect stems and are superficially similar to *E. biolettii*, but most others in the same area are shorter. A few collections are densely glandular but completely lack eglandular hairs (*e.g.*, Marin Co., *Elmer 4649*-CAS; San

Benito Co., *Eastwood 6743*-CAS); these are superficially like *E. biolettii*, but they produce relatively short stems, and small heads and leaves, and clearly belong with *E. petrophilus*.

b. **Erigeron petrophilus** E. Greene var. **sierrensis** Nesom, *var. nov.* TYPE: UNITED STATES. California: Yuba Co., Peterson Ridge Road, ca. 4 mi SE of Challenge, yellow pine forest, dry, red, rocky soil, 1000 m, 10 Aug 1983, *L. Ahart 4272* (HOLOTYPE: TEX!; Isotype: MO!).

Differt a *Erigeronte petrophilo* E. Greene var. *petrophilo* praecipue phyllariis absque apicibus purpuratis et habitationibus in sierris.

California endemic, northern Sierra Nevada Foothills (Map 8); ledges, other rocky sites in areas of pine and pine oak woods, most commonly on serpentine, 360-1910 m; Jul-Aug.

Additional collections examined: UNITED STATES. California: Butte Co.: Forbestown Res., ca. 5 mi NE of Forbestown, 24 Jul 1983, *Ahart 4206* (MO,TEX); near Pulga, 26 Jun 1951, *Howell 27525* (CAS); 2 mi W of Pulga, 19 Aug 1951, *Howell 28161* (CAS). El Dorado Co.: Junction Dam, W of Union Valley Reservoir, 20 Jul 1968, *Stebbins 6805* (CAS); foot of Jaybird Falls, above Jaybird Power House on canyon of Silver Creek, 20 Jul 1968, *Stebbins 6820* (CAS). Plumas Co.: Jamison Creek, 27 Jun 1951, *Howell 27625* (CAS); ca. 20 mi SW of Quincy, 1/4 mi E of Frenchman Hill, 27 Sep 1980, *Taylor et al. 3346A* (MO); Red Hill Lookout, ca. 3 air mi NE of Belden, 25 Aug 1981, *Taylor 4238* (MO); Rocky Point, head of No Ear Bar Trail, Middle Fork Feather River, among rocks in red clay, yellow pine forest with *Quercus kelloggii*, 21 Jul 1955, *Weatherby 1650* (UC).

c. **Erigeron petrophilus** E. Greene var. **viscidulus** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Erigeron inornatus* (A. Gray) A. Gray var. *viscidulus* A. Gray, *Syn. Fl.* 1(2):215. 1884. LECTOTYPE (designated here): UNITED STATES. California: [Siskyou Co.?], mountains about the headwaters of the Sacramento River, 1 Sep 1882, *C.G. Pringle 250* [or *14579*] (GH!; Isolectotypes: MO!,US). *Erigeron viscidulus* (A. Gray) E. Greene, Pittonia 1:174. 1888. Cronquist (1947) selected the Pringle collection over another syntype (*Kellogg & Harford s.n.*), but he did not choose between the GH and US specimens.

Erigeron decumbens Eastw., Bot. Gaz. (Crawfordsville) 41:290. 1906; not Nutt. 1840. TYPE: UNITED STATES. California: Siskyou Co., Mt. Eddy, 1400 m, 17 Aug 1903, *E.B. Copeland s.n.* (HOLOTYPE: CAS!).

Klamath Ranges of California and immediately adjacent Oregon (Map 8); open, rocky slopes, ledges, talus, sometimes on serpentine, 1490-2650 m; Jul-Sep.

Representative collections examined: UNITED STATES. California: Trinity Co.: Lower Canyon Lake, 5 Aug 1948, *Alexander 5400* (UC); summit of Scott Mtn., 2 Sep 1958, *Bacigalupi 6857* (JEPS); near top of Granite Peak, 8 Aug 1926, *Baker 267a* (UC); Trinity Alps, above Ward Lake, 19 Aug 1966, *Ferlatte 450* (JEPS); Siligo Peak-Summit Lake area, Dear Creek Pass, 16 Aug 1974, *Ferlatte 1660* (JEPS); summits near Dorleska, Jul 1909, *Hall 8588* (UC); Potato Mt., W slope, 2 Aug 1935, *Tracy 14437* (UC); Devil's Canyon Mts., head of White's Creek, 6 Aug 1935, *Tracy 14579* (JEPS,UC). Siskyou Co.: near Toad, S Siskyou County, 12 Aug 1911, *Alexander & Kellogg 307* (UC); Mt. Eddy, 30 Aug 1912, *Eastwood 2034* (UC); E side of Mt. Eddy, 28 Aug 1914, *Heller 11737* (UC); Scott Mts., Blue Point near Scott Mt. Public Campground, 8-9 Aug 1953, *Kellogg 123* (UC); side of Mt. Shasta, Jul [no year], *Lemmon s.n.* (UC); Caribou Lake, Salmon-Trinity Alps Primitive Area, 27 Jul 1955, *Wiggins 13560* (UC). Oregon: Jackson Co.: Mt. Ashland, S of Ashland, 29 Jun 1986, *Ertter 6457* (MO,UC); serpentine slopes of Red Mt., Siskyou Mts., 29 Jul 1935, *Thompson 12374* (CAS,MO,UC).

A collection of typical var. *viscidulus* by J.G. Lemmon (s.n. - JEPS,UC) from "Sierra Valley" is almost certainly mislabeled if the locality is meant to be from Sierra County.

The cauline vestiture of var. *viscidulus* is variable, comprising stiff hairs that primarily are spreading to slightly deflexed hairs but that vary to antrorsely appressed. Plants of this taxon with spreading vestiture were included by Cronquist (1947) within *Erigeron petrophilus*, and some (especially in Trinity Co.) even approach typical *E. petrophilus* in the length, looseness, and density of the nonglandular hairs, although none produce the corresponding dense glandularity. Plants with ascending stem hairs, including the lectotypic Pringle collection, were maintained by Cronquist as *E. inornatus* var. *viscidulus*. Part of the origin of the appressed stem hairs is perhaps found in the area of Scott Mountain (Trinity Co.), where apparent intermediates between var. *viscidulus* and *E. reductus* var. *reductus* occur. These plants seem to grade into typical var. *viscidulus* (with spreading vestiture). However, among numerous collections examined from Mt. Eddy (Siskyou Co.), well away from known populations of *E. reductus*, are plants with spreading stem hairs as well as others with appressed hairs. The morphology of such plants of var. *viscidulus* approaches that of *E. inornatus* and probably has provided the basis for considering the two taxa conspecific. The two, however, are sympatric and occur in generally the same kinds of habitats. While they are best regarded as separate species, it is possible that gene flow is occurring between them. Further, the variability accepted here within var. *viscidulus* leaves open the possibility that it may be polyphyletic in origin.

12. **Erigeron reductus** (Cronq.) Nesom

Erigeron reductus (Cronq.) Nesom, *comb. et stat. nov.* BASIONYM: *Erigeron inornatus* (A. Gray) A. Gray var. *reductus* Cronq., Brittonia 6:288. 1947. TYPE: UNITED STATES. California: Placer Co., on rocks, Yuba River near Cisco, 5600 ft, Transition Zone, 3 Jul 1910, *H.M. Hall 8741* (HOLOTYPE: UC!; Isotype: US!).

Stems 8-20(-30) cm tall, basally erect or ascending, few, arising from long, slender, rhizomelike caudex branches, glabrous. Leaves linear, 8-25(-35) mm long, 0.5-1.0(-1.5) mm wide, glabrous or sparsely strigose on the lamina, the margins prominently ascending ciliate with thin based hairs. Heads 8-10 mm wide, solitary or 2-4 on short peduncles; phyllaries minutely but prominently granular-glandular, without other hairs, the inner 4.0-6.0 mm long. Ray flowers absent. Disc corollas 3.5-4.5 mm long. Achenes 2.2-2.8 mm long; pappus bristles 20-61.

Erigeron reductus is composed of two allopatric but very similar entities united by their distinctive habit, highly reduced vestiture, and rayless heads. Both taxa have previously been treated as varieties of *E. inornatus*, but there is evidence that *E. inornatus* and var. *reductus* intergrade in Trinity Co. (see comments below). Cronquist (1947) also recognized var. *reductus* and var. *angustatus* as most closely related to each other, although his concept of the latter was broader than that here (see comment below). As treated here, *E. reductus* has a geographic distribution similar to that of *E. petrophilus*, forming a northern "hook" around the Sacramento Valley (Map 9).

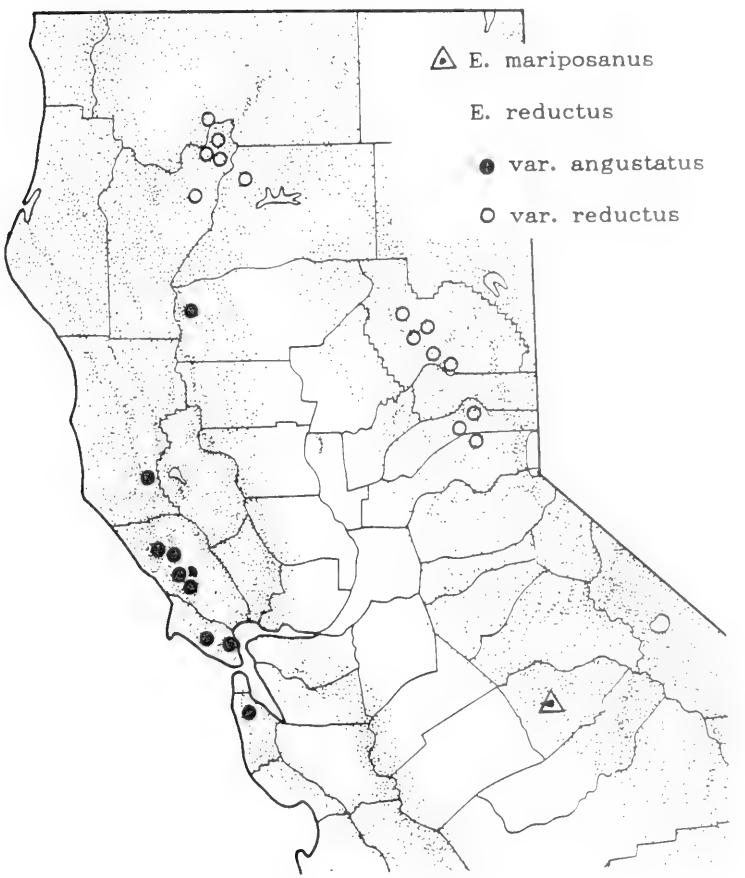
Key to the varieties of *E. reductus*

1. Phyllary apices purplish (variably so in the Tamalpais region); pappus bristles (38-)46-61. ..... var. *angustatus*

1. Phyllary apices greenish; pappus bristles 20-30. ..... var. *reductus*

a. **Erigeron reductus** (Cronq.) Nesom var. **angustatus** (A. Gray) Nesom

Erigeron reductus (Cronq.) Nesom var. **angustatus** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Erigeron inornatus* (A. Gray) A. Gray var. *angustatus* A. Gray, *Syn. Fl.* 1(2):215. 1884. LECTOTYPE (Cronquist 1947): UNITED STATES. California: Mendocino Co., Red Mountain, 2 Jul 1869, *A. Kellogg & Harford 399* (GH!; Isolectotype: US!). Cronquist noted that the CAS sheet of *Kellogg & Harford 399* bears a specimen of *E. biolettii*. In the original description, Gray also cited "Greene, Napa Co." (Greene's no. *339* at GH), but this is *E. angustatus*, the species.



Map 9. *Erigeron reductus* and *E. mariposanus*.

California endemic, San Francisco Bay area, Outer and High North Coast Ranges (Map 9); rocky sites, commonly on serpentine, often in pine or pine-oak woods, 600-1360 m; Jun-Aug.

Specimens examined: UNITED STATES. California: Marin Co.: Carson Ridge summit at head of Big Carson Canyon, 16 Jul 1943, *Bacigalupi 2772* (DS); Westpoint Road, Tamalpais, Jul 1907, *K. Brandegee s.n.* (UC); Mt. Tamalpais, 2 Aug 1896, *Eastwood s.n.* (JEPS,UC), Sep 1898, *Eastwood s.n.* (UC), 29 Jul 1912, *Eastwood 1518* (CAS,MO,UC); burned area S of Barth's Retreat, Mt. Tamalpais, 7 Jul 1946, *Howell 22197* (CAS,DS,UC); N end of Tiburon Peninsula, above Vista de la Bahia, 18 Jun 1972, *Howell 48875* (CAS); El Campo, Jul 1891, *Michener & Bioletti 1133a* (ND-G); S side of Mt. Tamalpais, 14 Jul 1913, *Suksdorf 538* (MO). Mendocino Co.: Little Red Mt., 6 Aug 1932, *Tracy 10306* (JEPS,UC), 7 Aug 1932, *Tracy 10316* (UC); Little Red Mt., 6 Aug 1932, *Jepson 16504* (JEPS) and *16502* (JEPS); Red Mt. near Ukiah, 24 Jul 1909, *McMurphy s.n.* (DS); Red Mt. N, 1 Jul 1982, *Smith & Wheeler 7563* (CAS) and *7576* (CAS). San Mateo Co.: Crystal Springs Lake, 9 Nov 1930, *Howell s.n.* (CAS). Sonoma Co.: 3 mi N of Occidental on Bohemian Hwy, 5 Jun 1981, *Best s.n.* (CAS); Monte Rio, Aug 1920, *Campbell s.n.* (CAS); Pepperwood Ranch, Franz Valley Road, 6 Jun 1981, *DeNevers 1451* (CAS); Pepperwood Ranch, Dentist's Lake, 20 Jun 1981, *DeNevers 1634* (CAS; 2 mi E of Occidental, 5 Jul 1946, *Mason & Grant 12898* (DS); unnamed ridge on W side of Dry Creek Valley, N of Crane Creek, S of Bradford Mt., 30 Jun 1985, *Raiche 50565* (CAS). Tehama Co.: serpentine slope on NW side of Tedoc Mt., 17 Jun 1972, *Heckard 2962* (JEPS).

In Cronquist's view (1947), this taxon included *Erigeron angustatus* and was subsumed as a variety of *E. inornatus*. *Erigeron angustatus* (the species) is different in habit from *E. reductus* and has a narrower geographic range.

b. *Erigeron reductus* (Cronq.) Nesom var. *reductus*

California endemic, southern Klamath Ranges, northern High Sierra Nevada (Map 9); crevices and open, rocky sites, commonly on serpentine, 760-1940 (-2360) m; Jun-Aug.

Specimens examined: UNITED STATES. California: Nevada Co.: 5.6 mi E of Emigrant Gap on US Hwy 40, 30 Jun 1940, *Beach 800* (CAS,JEPS,LL,UC); above Meadow Lake, 7 Aug 1892, *Sonne 5* (UC, on sheet with *E. miser*). Plumas Co.: slopes of Mt. Elwell above Long Lake, 10 Jul 1927, *Bacigalupi 1688* (DS); Feather River region, Summit Peak above Round Lake, 15 Jul 1920, *Head s.n.* (CAS); Feather River region, Lake Center Camp, 15 Jul 1921, *Head s.n.* (CAS); Jamison Lake, 5 Sep 1932, *Rose 32621* (CAS). Shasta Co.: Lamoine, 16 Jul 1910, *Blankinship s.n.* (JEPS). Siskyou Co.: Trinity Mts., road to Mumbo Basin, just below summit, 29 Jul 1967, *McClintock s.n.* (CAS).

Trinity Co.: 2 mi S of Scott Mtn Forest Camp, on Scott Mtn. Road, 3 Aug 1955, *Barbe 336* (UC); N of Coffee Creek, 16 Aug 1988, *Dean 175* (UC); SW of Peanut, 17 Jul 1955, *Howell 30701* (CAS); 1 mi S of Scott Mt. Summit, 20 Jul 1949, *Keck 6377* (DS-2 sheets); head of Rush Creek, 20 Jul 1914, *Yates 541* (JEPS).

In Trinity County, plants of some collections of *Erigeron reductus* appear to vary toward *E. inornatus* (and vice versa), but identifications can generally be made on the basis of the habit. The stems of *E. reductus* usually arise singly from slender, rhizomelike caudex branches, while the stems of *E. inornatus* are more numerous and arise from a woodier base, which is rarely collected. The plants in the northern segment of var. *reductus* range somewhat taller than typical, perhaps reflecting genetic input from *E. inornatus*.

13. **Erigeron serpentinus** Nesom

Erigeron serpentinus Nesom, *sp. nov.* TYPE: UNITED STATES. California: Sonoma Co., Layton Mine, Austin Creek, serpentine soil, 30 May 1947, *F.W. Hoffman 558* (HOLOTYPE: UC!).

Differt a *Erigeronte angustato* E. Greene floribus radii carentibus et capitulis minoribus. Differt a *Erigeronte folioso* Nutt. var. *franciscensi* Nesom ac var. *mendocino* (E. Greene) Nesom caulibus numerosis ad apicem radicis statim orientibus, caulibus ac foliis glabris, et floribus radii paucioribus.

Stems 4-5 dm tall, erect, numerous, arising directly from the crown atop a woody taproot. Stems and leaves mostly glabrous, leaves sparsely ascending ciliate with thin based hairs. Leaves linear, 2-4 cm long, 0.6-0.8 mm wide. Heads 9-12 mm wide; phyllaries minutely granular-glandular, with very few, minute, appressed non-glandular hairs, the inner 4.5-5.0 mm long. Ray flowers 9-13, the corollas 7-8 mm long, 1.5-2.5 mm wide, drying blue. Disc corollas 3.2-4.0 mm long. Mature achenes not seen; pappus bristles 26-32.

California endemic, North Coast Ranges in Sonoma Co., vicinity of Layton Mine along Austin Creek (Map 1); shrubby vegetation over serpentine, ca. 400-600 m; May-Aug.

Additional collection examined: UNITED STATES. California: Sonoma Co., near seep above Austin Creek, (below Layton Mine buildings), the Cedars, occasional in chaparral on serpentine, usually close to moisture, 6 Aug 1983, *Raiche 90587* (JEPS).

Erigeron serpentinus apparently is a narrow endemic restricted to serpentine outcrops in central Sonoma County. It is similar in habit and vestiture to *E. angustatus*, and probably most closely related to it, but plants of the latter

are rayless and they have larger heads and longer disc corollas. *Erigeron angustatus* also is endemic to serpentine exposures of the same region, although it is somewhat more widespread (Map 1). The collection information for *E. serpentinus* (*30587*) notes that the plants "apparently spread by rhizomes," but the specimens do not show this. Instead, the numerous stems on the specimens collected arise densely and immediately erect from the crown.

Among the radiate taxa with glabrous to sparse and appressed stem vestiture, the geographical range of *Erigeron serpentinus* occupies a region between that of *E. foliosus* var. *franciscensis* and var. *mendocinus*. It is strikingly different from both of the latter in vestiture as well as head morphology; scattered individuals of var. *foliosus* approach *E. serpentinus* in habit, or in vestiture, or in the reduced number of ray flowers, but I have seen no specimen of var. *foliosus* that combines the distinctive features of *E. serpentinus*.

SPECIES PERIPHERAL TO SECT. *LINEARIFOLII*

In contrast to the group of taxa closely centered around *Erigeron foliosus*, the other species that most closely resemble them differ in significant features. These latter were included with the *E. foliosus* group in *Erigeron* sect. *Linearifolii* (Nesom 1989), but after detailed study of the typical part of the section, it is more difficult to retain the peripheral elements together with the typical. The former are included and briefly treated here, as they may prove to be closely related, but it would not be surprising if they were found to represent, even among themselves, a diverse group of taxa most closely related to disparate phyletic lines within the genus.

1. *Erigeron hyssopifolius* Michx.

Erigeron hyssopifolius Michx., *Fl. Bor. Amer.* 2:123. 1803. TYPE: CANADA. Quebec: Lake Mistassini, *A. Michaux s.n.* (GH photo!, UC photo, US photo!).

Aster graminifolius Banks *ex* Pursh, *Fl. Amer. Septent.* 2:545. 1814. TYPE: [Canada]. at Hudson's Bay, Aug, Sep, [year not specified], *Dr. Richardson s.n.* ("herb. Banks," not seen). *Galatella graminifolia* (Banks *ex* Pursh) W.J. Hook., *Fl. Bor. Amer.* 2:15. 1834.

Southeastern Canada and adjacent northeastern United States. Chromosome number, n=9 (Montgomery & Yang 1960; Gervais 1979; Löve & Löve 1980; Morton 1981; Semple 1980; Löve & Löve 1982; Chinnappa & Chmielewski 1987).

Two varieties have been recognized within *Erigeron hyssopifolius*, but I have not attempted to evaluate their status. Cronquist (1947) included the

species within sect. *Pycnophyllum* (the *E. foliosus* group) on account of its narrow leaves densely arranged on the stems, occasionally resembling *E. foliosus* var. *confinis*, but as he noted (p. 277), "it certainly is not approached by anything else in the section." It differs strongly from the species centered around *E. foliosus* in several features: cauline leaves abruptly and sharply reduced in size, the heads solitary on bracteate peduncles 5-10 cm above the level of the leaves; 3 nerved phyllaries all nearly equal in length; and ligules of the ray corollas not coiling. Should *E. hyssopifolius* prove to be only distantly related to the *E. foliosus* group, *Erigeron* sect. *Linearifolii* probably would comprise only *E. hyssopifolius*, and sect. *Pycnophyllum* would be the correct name for the numerous taxa of the *E. foliosus* group.

2. *Erigeron lepidopodus* (B. Rob. & Fern.) Nesom

Erigeron lepidopodus (B. Rob. & Fern.) Nesom, Sida 9:31. 1981. BASIONYM: *Aster lepidopodus* B. Rob. & Fern., Proc. Amer. Acad. Arts 30:117. 1894. TYPE: MEXICO. Chihuahua: Pine forests about Chuchuichupa, 14 Jun 1891, *C.V. Hartman 697* (HOLOTYPE: GH!; Isotypes: US-2 sheets!).

Central Chihuahua, México. Chromosome number, n=9 (R.W. Spellenberg unpubl.).

Erigeron lepidopodus and *E. rhizomatus* Cronq. are closely similar in geographic range and morphology, and they are almost certainly related as sister species. Plants of both produce stems from rhizomelike caudex branches, without clustered basal leaves, but both produce long, noncoiling ray corollas and phyllaries that are nearly equal in length, unlike any taxa of the *E. foliosus* group. Cronquist (1947) placed *E. rhizomatus* as a member of *Erigeron* sect. *Wyomingia* (A. Nelson) Cronq.

3. *Erigeron rhizomatus* Cronq.

Erigeron rhizomatus Cronq., Brittonia 6:274. 1947. TYPE: UNITED STATES. New Mexico: McKinley Co., canyon S of Fort Wingate, 16 May 1943, *Ripley & Barneby 5272* (HOLOTYPE: NY!).

Southwestern New Mexico, United States. Chromosome number, n=9 (Ward & Spellenberg 1986).

4. *Erigeron chiangii* Nesom

Erigeron chiangii Nesom, Sida 8:65. 1979. TYPE: MEXICO. Coahuila: Cañon de la Madera, Sierra de la Madera, 29 Mar 1975, *T. Wendt & E. Lott 842* (HOLOTYPE: LL!).

Central to northern Coahuila, México. Chromosome number, n=18 (Nesom 1979).

The relationships of *Erigeron chiangii* and *E. scoparioides* Nesom were not clearly understood at the times of their separate publications, but it now appears that they may be sister species. Both have a habit generally characteristic of the *E. foliosus* group, although the basal leaves of *E. chiangii* are sometimes persistent. The latter was originally compared to the *E. foliosus* group, but both it and *E. scoparioides* produce features anomalous among those western species. Their potential relationship, however, to any more geographically proximal species is equally as obscure.

5. *Erigeron scoparioides* Nesom

Erigeron scoparioides Nesom, Phytologia 66:488. 1989. TYPE: MEXICO. Tamaulipas: Mpio. Bustamante, ca. 1 mi NW of Hwy 101 on road to Bustamante, pine-juniper woodlands, 1680 m, 2 Aug 1983, *G. Nesom 4785* (HOLOTYPE: TEX!; Isotypes: ANSM!,CAS!,GH!,MEXU!,MICH!,NY!, US!).

Westcentral Tamaulipas, México.

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A NEW SPECIES OF *CASTILLEJA* (SCROPHULARIACEAE) FROM SOUTHCENTRAL TEXAS WITH COMMENTS ON OTHER TEXAS TAXA

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ABSTRACT

Castilleja genevievana *sp. nov.* is described from Crockett, Pecos, Upton, and Val Verde cos., Texas, and one closely adjacent locality in Coahuila, México. It is most closely related to *C. integra* and *C. purpurea* var. *citrina* but is allopatric with both and morphologically distinctive in its entire leaves, unbranched trichomes, and yellow floral bracts and calyces. *Castilleja wootonii* (the type from southeastern New Mexico) is the correct name for the species in Jeff Davis Co., Texas, previously known as *C. ciliata* and assumed to be a narrow endemic. *Castilleja elongata*, which has been recognized primarily from Brewster Co., Texas, and a proposed but yet unpublished species endemic to Jeff Davis Co. are interpreted as merely intergrading elements of the widespread and variable *C. integra*. *Castilleja latebracteata* (the type from Texas) is a synonym of *Castilleja rigida* (the type from Chihuahua), a species primarily distributed in northern México. *Castilleja tortifolia* (the type from Texas) is conspecific with the earlier named *C. mexicana*, also most abundant in northern México.

KEY WORDS: *Castilleja*, Scrophulariaceae, Texas, México

I. A new species from southcentral Texas

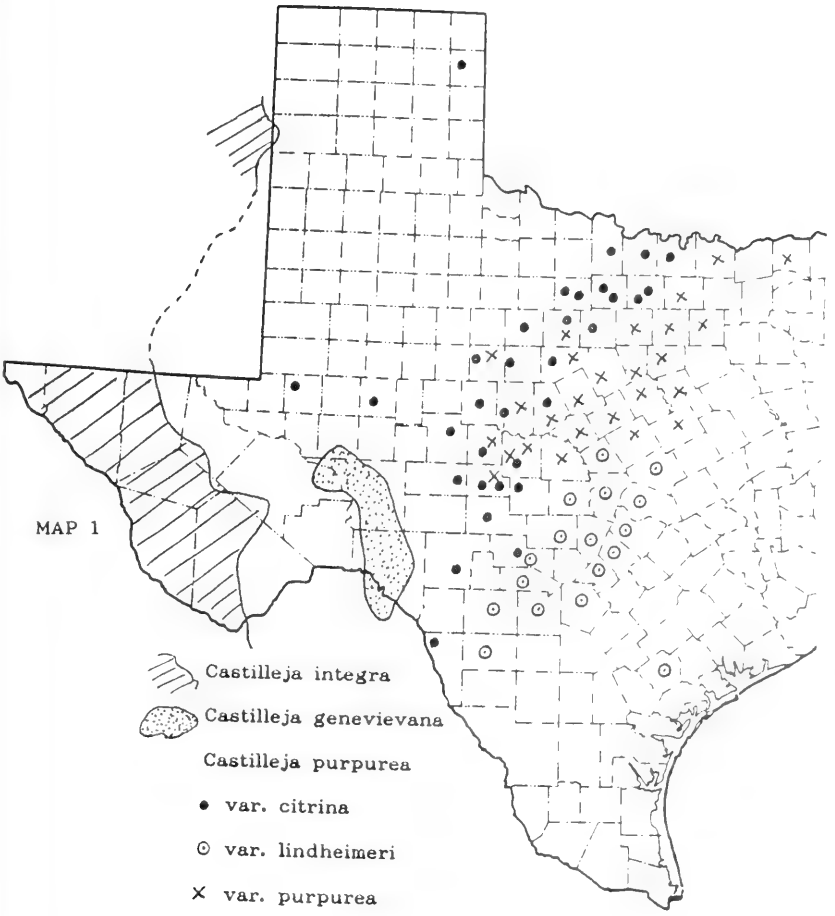
In his taxonomic treatment of Texas *Castilleja*, Holmgren (1970) noted that a population of *C. integra* A. Gray in Crockett Co. represented a geographically outlying segment different from the rest of the species in its "yellowish inflorescences and shorter floral measurements" and might prove to be distinct. These yellow flowered plants occur on the western edge of the Edward's Plateau of southcentral Texas, where they are now known from Pecos, Upton, and Val Verde cos., as well as Crockett Co. and from one closely adjacent

locality in Coahuila, México (Map 1). They are completely geographically separated from *C. integra*, which in Texas is restricted to the trans-Pecos area and which produces red bracts and calyces as well as a different vestiture. The Crockett Co. plants are more similar in vestiture, bracteal morphology, and coloration to *C. purpurea* (Nutt.) G. Don var. *citrina* (Penn.) Shinners, which occurs primarily from central Texas northward and which has a different leaf and floral morphology. Specimens of these geographically intermediate plants have most often been identified with caveats as *C. integra* or as *C. purpurea* var. *citrina*, and indeed they appear to be most closely related to both of these latter two taxa. As discussed below, however, they are distinct from both and may be justifiably regarded as a separate species.

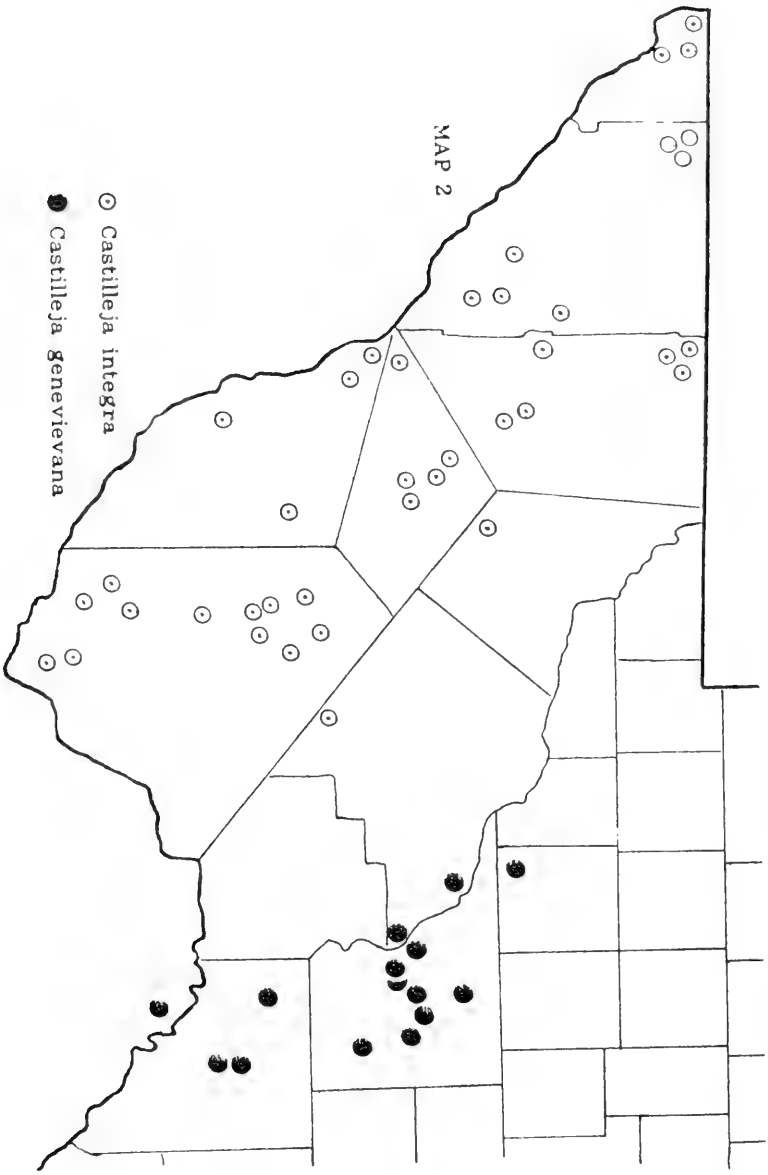
Castilleja genevievana Nesom, *sp. nov.* TYPE: UNITED STATES. Texas: Crockett Co., Hwy 290, 1.5 mi WSW of jct with Hwy I-10, ca. 24 mi W of Ozona (jct of I-10 and Hwy 163); area of steep limestone hills with dominant junipers, 2500 ft elevation, ca. 80 plants in an area of ca. 250 square yards, road bank and among scattered shrubs to fenceline; 5 April 1992, *Guy & Genevieve Nesom 03* with Julia Nesom (HOLOTYPE: TEX!; Isotypes: ANSM!,BRIT!,COLO!,GH!,MO!,NMC!,NY!,PH!,SRSC!,SWT!, TAES!,UC!,UNM!,UTEP!).

Castillejae integrae A. Gray ac *C. purpureae* (Nutt.) G. Don var. *citrinae* (Penn.) Shinners similis sed ab uterque proprius habitatione et distributione geographica, vestimento trichomatum non ramosis, foliis plerumque integris, bracteis ac calycibus flavis, bracteorum lobis anguste lanceolatis, et corollarum lobis infernis comparate brevioribus.

Plants perennial from strongly developed woody roots. Stems branched at base, the branches erect or ascending, 15-45 cm tall, loosely lanate with a moderate to dense investment of multicellular, unbranched, flattened, and vitreous hairs 0.5-2.0 mm long, these most commonly becoming somewhat tangled, often deflexed or retrorsely oriented, glandular hairs absent. Leaves linear-lanceolate, strongly 3 veined, 3-7 cm long, 4-8 mm wide, entire or the uppermost (rarely from midstem upwards) with a pair of linear or filiform lobes originating on the distal third of the blade, the adaxial surfaces moderately to densely invested with short, stiffly erect hairs, the abaxial surfaces glabrous or very sparsely hairy, margins densely long ciliate or at least with hairs distinctly longer than on the surfaces. Mature inflorescence 5-10 cm long, elongating at fruit maturity to 10-20 cm. Floral bracts 2-3 cm long, yellow-green on the basal 2/3, distally yellow varying uncommonly to orangish yellow or rarely to red, 8-12 mm wide, ovate to broadly oblanceolate obovate, entire or with a pair



Map 1. Distribution of *Castilleja purpurea*, *C. genevievana*, and *C. integra* in Texas.



Map 2. Detailed distribution of *Castilleja genevievana* and *C. integra* in Texas. Two collections of *C. integra* from Deaf Smith County are not shown.

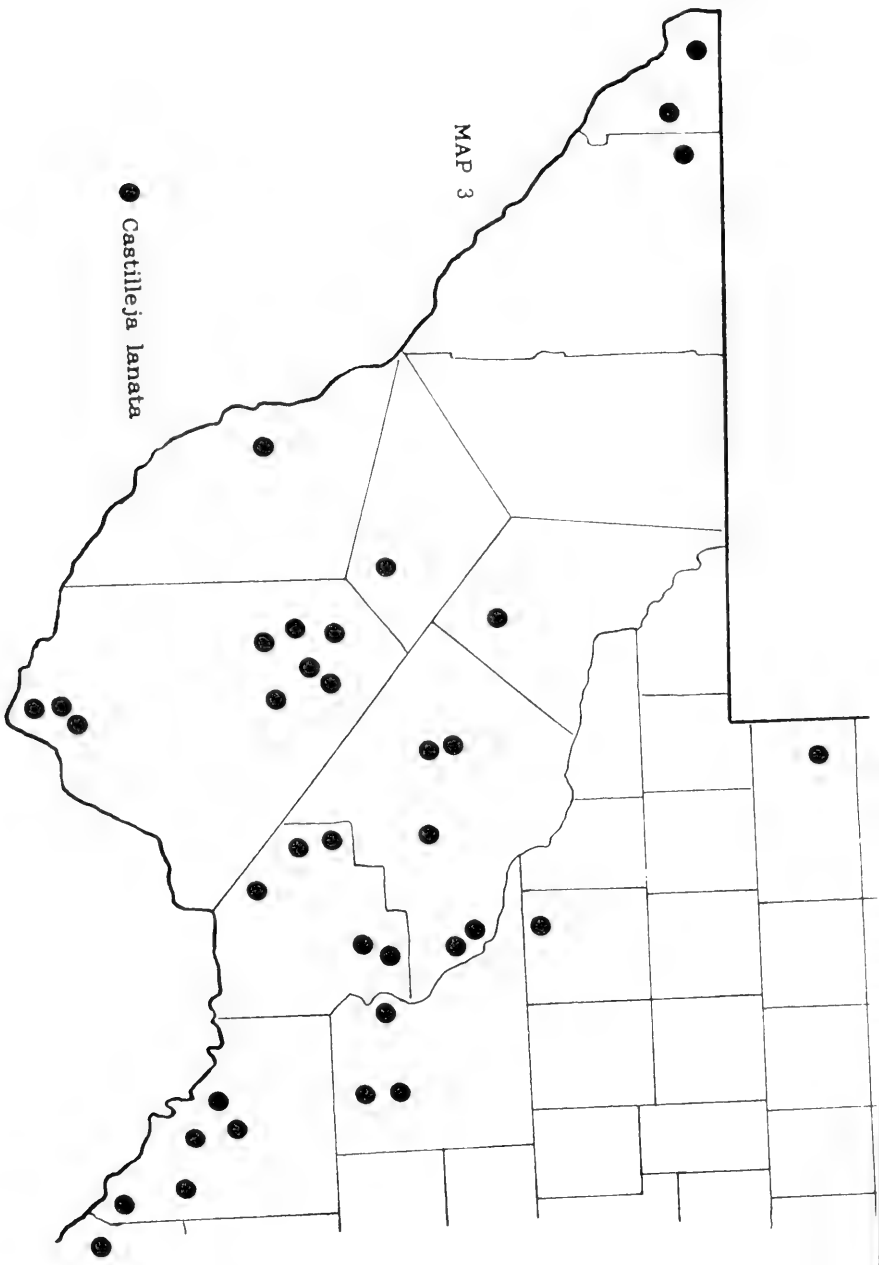
of narrowly lanceolate lobes originating slightly above the middle, the upper bracts densely stipitate glandular, without other hairs. Calyces 23-27 mm long, yellow to orangish yellow at least distally, the primary lobes 10-15 mm long, the secondary lobes 4-7 mm long, the primary lobes 1.7-2.5 times longer, densely stipitate glandular distally, without other hairs. Corollas 24-31 mm long, the 3 teeth of the lower lip 2-4 mm long, usually distinctly thickened, distally yellow, the tube light yellow, the galea 7-12 mm long, 1/3-2/5 the corolla length, with yellow to white or pink margins, the dorsal surface green to yellowish, densely short glandular; stigma and style exserted 1-4 mm, the stigma weakly to strongly recurved at maturity, with ovate branches. Mature fruits ovate, 10-15 mm long, 6-8 mm wide. Color photograph in Warnock (1970, p. 125, no. 4), as "*C. citrina.*"

Rocky, limestone hills of southcentral Texas and adjacent Coahuila, México, vegetation dominated by juniper, 1700-2800 ft: midMarch through midJune.

Additional specimens examined: MEXICO. Coahuila: Mpio. Villa Acuña, open country between Rancho Santo Domingo and Hacienda Piedra Blanca, 4 Jul 1936, *Wynd & Mueller 487* (GH).

UNITED STATES. Texas: Crockett Co.: 23 mi W of Ozona, 30 Apr 1970, *Correll & Correll 38524* (LL); Salviastrum Mesa, 32 airline mi NW of Ozona, frequent on talus slope, 23 Apr 1947, *Cory 53424* (SMU); 25 mi W of Ozona, 7 May 1947, *McVaugh 8208* (SMU,TEX-2 sheets); Read Ranch, 14 mi SE of Ozona, 3 Jul 1961, *Read A-18* (SRSC); 7 mi S of Ozona on Hwy 163, 1 Jun 1963, *Read 141* (SRSC); 15 mi E of Pecos River on Hwy 290, top of Batchlor Hill, 15 Apr 1964, *Read 593, 594*, and *595* (SRSC); 20 mi W of Ozona, 14 Apr 1949, *Tharp & Havard 49358* (TEX); 14.8 mi W of Ozona, 2400 ft, 14 Mar 1949, *Turner & Warnock 274* (LL,SMU,SRSC); 14 mi N of Juno in limestone soil, 2000 ft, 1 May 1949, *Warnock & Turner 765* (SMU,SRSC); 5 mi E of Pecos River on Hwy 290, limestone bluff above Live Oak Creek, 11 May 1947, *Whitehouse 18689* (SMU). Pecos Co.: Sheffield, 20 Apr 1931, *Jones 18287* (MO); 14 mi N of Sheffield, 1 Jun 1957, *Warnock 14907* (LL,SRSC). Upton Co., no other locality data, 7 May 1938, *Cory s.n.* (TEX). Val Verde Co.: limestone bluffs above Pecos River, 26 mi N of Langtry, 30 Mar 1947, *Warnock 47-279* (SRSC-2 sheets); 2 mi N of Devil's River crossing along Hwy 163, 1 May 1949, *Warnock & Turner 759* (SRSC); 22 mi N of Comstock on Hwy 163, 1 May 1949, *Warnock & Turner 765* (SRSC).

The new species is named for my yellow haired daughter, an avid outdoorsman and happy participant in the collection of the type. *Castilleja genevievana* is restricted to the southwestern corner of the Edward's Plateau (Maps 1 and 2). At the western margin of its range, there is a corresponding, abrupt vegetational discontinuity at the edge of the juniper dominated landscape moving westward into areas of *Larrea*. The geographic position of *C. genevievana* intermediate between its two close relatives is matched by its habitats at an intermediate range of elevation (1700-2800 feet). *Castilleja integra* occurs at



Map 3. Distribution of *Castilleja lanata* in Texas.

elevations of (2800-)3200-8600 feet in Texas; *C. purpurea* ranges over a number of different vegetational zones in Texas but occurs at 300-1750 feet in elevation, with rare outlyers (var. *citrina* in Ector and Schleicher Cos.) up to 2500 feet.

Castilleja genevievana, *C. purpurea*, and *C. integra* are similar in their perennial duration, lightly lanate stem vestiture, 3 veined leaves with distinctly reduced adaxial vestiture, and the dimensions and morphology of their bracts and flowers. Further, the stem and leaf hairs of all three have a strong tendency to be retrorsely oriented. *Castilleja genevievana* differs from *C. integra* in the yellow (vs. red) pigmentation of its floral bracts and calyces and in its vestiture of unbranched hairs (see discussion below, following *C. elongata*). In contrast, *C. genevievana* is similar to *C. purpurea* var. *citrina* in its pigmentation and unbranched hairs, as well as the narrowly lanceolate bracteal lobes. It differs from *C. purpurea* in its entire leaves, although rare plants of *C. genevievana* may produce lobed leaves on the upper half of the stems.

The floral bracts of most plants of *Castilleja genevievana* are distally yellow; they vary to orangish yellow or rarely slightly orangish (label data of *McVaugh 8208*) or rarely vary within populations from "yellow, orange, to scarlet" (label data of *Warnock 47-279*) or from yellow ("common," *Read 593*) to yellowish orange to reddish ("rare," *Read 594*) or orangish ("rare," *Read 595*). Of the ca. 80 plants of the population from which the type collection was made, all except two produced bracts and calyces with a bright, lemon-yellow color. The two exceptions were distinctly orangish.

Castilleja genevievana is probably most closely related to *C. purpurea* var. *citrina*, in view of their predominately yellow pigmentation (almost certainly a specialization within this group of related taxa). *Castilleja genevievana* and var. *citrina* produce only unbranched hairs (an unspecialized condition, see discussion below) and never bear the distinctive branched hairs characteristic of *C. integra* and *C. lanata* A. Gray. The new species might have been reasonably included as a fourth variety of *C. purpurea*, closely related to var. *citrina*, but the other three recognized varieties differ from *C. genevievana* in their consistent production of lobed leaves (1-2[-3] pairs of lobes) from the bottom to top of the stems (vs. leaves entire in *C. genevievana*) and corollas with the lower lip of three thin and at least distally petaloid, ovate lobes 4-7 mm long (vs. thickened, lanceolate, and 2-4 mm in *C. genevievana*). Further observations on variation within *C. purpurea* are given below.

According to Holmgren (1971, p. 26), "Most of the closely related species in *Castilleja* probably could not stand the test of sympatric maintenance." The same may be true for *C. integra*, *C. purpurea*, and *C. genevievana*, because they are geographically separated. Each, however, is immediately distinguishable by morphological features, and all three can justifiably be recognized at an equivalent taxonomic rank.

II. Variation in *Castilleja purpurea* in Texas

The geographic range of *Castilleja purpurea* extends from central Texas (Map 1) through Oklahoma to southern Kansas. Yellow bracted plants (var. *citrina*) occur from Texas to the northern extremity of the range of the species; purple bracted ones (var. *purpurea*) are found from southern Oklahoma to northcentral Texas; red to orange bracted ones (var. *lindheimeri* [A. Gray] Shinners) are endemic to southcentral Texas.

Plants within single populations of var. *purpurea* are strikingly variable in coloration: the bracts and calyces are predominately pinkish purple but vary from red, to reddish orange, burnt orange, peach, light yellow, creamy (very light orange-yellow), and rarely white. Similar variation has been noted on the labels of collections from Eastland Co. (*McVaugh 8338*-TEX), Hamilton Co. (*Correll & Johnston 21098*-LL), Hill Co. (*Lundell 11309, 11310, 11311, 11312, 11313, 11314*-all LL), McLennan Co. (*Nesom 7276*-TEX), and other localities. In addition, a great deal of infrapopulation variation occurs in bract and flower size: the bracts 20-40 mm long, the corollas 25-40 mm long. Similar variation in size also occurs in the other varieties of *Castilleja purpurea*.

Plants of var. *lindheimeri* produce predominately reddish orange to orange bracts and calyces, but a red color is commonly produced similar to that of typical *Castilleja integra*. A citrinalike yellow occurs rarely: in one population (Comal Co., *Nesom 7284*-TEX), one plant with three branches of orange flowers also produced a single branch with yellow flowers; in another (Travis Co., *Nesom 7275*-TEX), two yellow-bracted plants occurred in a predominately red bracted population, and several individuals were intermediate. I have tentatively treated these as populational variants of var. *lindheimeri*. The typical coloration of var. *lindheimeri* might be regarded as only a small subset of that occurring in var. *purpurea* (except for the citrina yellow, which does not appear as normal variation within var. *purpurea*), but there appears to be a relatively abrupt geographic transition between the two (Map 1), and they can be justifiably maintained as weakly delimited varieties.

Populations of var. *citrina* are considerably less variable in coloration than in the other two varieties of *Castilleja purpurea*. The bracts and calyces are tipped with bright lemon-yellow, uncommonly with yellowish orange. In the southern portion of the range of the species, var. *citrina* and var. *lindheimeri* apparently are essentially allopatric or nearly so (Map 1); the ranges of var. *citrina* and var. *purpurea*, however, more closely approach each other. In McCulloch and Menard cos., near the juncture of the two taxa, populations of var. *purpurea* are even more variable than normal and include plants with yellow bracts and calyces that do not appear elsewhere in its range. One such population (3 mi N of Brady, McCulloch Co., *Nesom 7282*-TEX) produced an astounding array of individuals with red, pink, purple, orange, yellow, and white bracts and calyces. Along Highway 190 for about 25 miles, from

near Brady (McCulloch Co.) towards Menard (Menard Co.), populations of normally variable var. *purpurea* alternate with presumably hybrid populations producing yellow variants. Westward from about six miles east of Menard, all plants are yellow bracted var. *citrina*, without any evidence of introgression from var. *purpurea*.

Genes of var. *citrina* apparently are present in populations of var. *purpurea* in their region of contact, but not vice versa, as if var. *citrina* were serving only as the pollen parent of the putative hybrids. Chromosome counts and field observations at additional localities will be necessary in a more critical assessment of the relationship between all three varieties of *Castilleja purpurea*.

Castilleja purpurea (var. *purpurea* and var. *lindheimeri*) commonly grows with *C. indivisa* Engelm. along the eastern margin of the Edward's Plateau. The latter is native to eastern Texas, southeastern Oklahoma, and western Louisiana but is now also widely seeded by the Texas Highway Department for its beauty along roadsides. *Castilleja indivisa* is closely related to the widespread Mexican species *C. scorzoneraefolia* Kunth and relatives (see Nesom 1992), including the Texas species *C. rigida* Eastwood (see below), but where *C. indivisa* grows with *C. purpurea*, hybrids between the two species are common. At one such roadside locality in Coryell County (*Nesom 7279/7280*-TEX), intermediates and apparent backcrosses toward both parents produced a wide range of combinations of morphological features, including bract and calyx color, corolla, calyx, and leaf morphology, duration (judging from the root development), and habit. At several localities in Hays County (e.g., *Nesom 7283*-TEX), where *C. indivisa* was not artificially seeded, hybrids between it and *C. purpurea* were relatively common, and no individuals of the former without genetic influence of the latter could be found.

III. Two putatively rare and endemic taxa of trans-Pecos Texas

The status of *Castilleja elongata* Pennell

In his study of the Scrophulariaceae of trans-Pecos Texas, Pennell (1940) described *Castilleja elongata*, which he considered to be a narrowly endemic species. It has generally been acknowledged to occur on Emory Peak of the Chisos Mountains in Brewster Co., although specimens from the Davis Mountains of Jeff Davis Co. have also been identified as *C. elongata*.

The original description of *Castilleja elongata* was based only on the type specimen, and Pennell's sole comment regarding it (1940, p. 307) was that it "would seem to be the representative of the group of *Castilleja miniata* Dougl. [*ex* Hook.] in the mountains of the Big Bend district of southern Trans-Pecos Texas." In contrast, with many collections now available for study from trans-Pecos Texas, I can find no feature to separate *C. elongata* from the widespread

and variable *C. integra*. Holmgren (1970) distinguished *C. elongata* from *C. integra* by its stems "finely villose" (vs. "whitish-tomentose or lanate") and its bracts "not glandular-pubescent" (vs. "glandular-puberulent on the colored portions"). All *C. integra*-like plants of Brewster Co., however, produce bracts that are prominently glandular on the distal portion with short, capitate hairs, these usually mixed with nonglandular hairs, and the stems of such plants are highly variable in the amount of vestiture produced. In the present study, I have examined 58 collections (not including duplicates) of *C. integra* from Brewster Co.; fifteen of these are from the Chisos Mountains.

Castilleja integra in Brewster Co. occurs at 3600-6200 feet, outside of the Chisos Mountains, where it occurs at 5500-7500 feet; elsewhere in Texas it has been collected at elevations of 5000-7500(-8600) feet in Jeff Davis Co., 4150-7500(-8000) feet in Culberson Co., and 5900-7000 feet in El Paso Co. At the higher elevations, plants tend to be more variable in height, ranging somewhat taller (to 1 meter or more in the Chisos Mountains), with a somewhat reduced amount of vestiture, and they produce calyces and corollas that range to near the low end of the range of length for the species. Within these atypical populations, however, the intergradation in stature, vestiture, and floral size with plants of lower elevations appears to be complete.

The same phenomena were observed in *Castilleja integra* in New Mexico by Standley (1909, p. 86), who noted that in the Organ Mountains, "it grows at an altitude of about 6000 feet, on shaded slopes, where it is a tall plant and but little branched. Farther north, in the region about Santa Fe it is very low and much branched, growing on the open mesas and foothills, but at about the same altitude. The size of the flowers and bracts varies noticeably in different plants ... Most of these variations, perhaps, are due to climatic conditions, especially temperature and the water content of the soil."

Castilleja integra occurs from Arizona to Colorado, New Mexico, and Texas and in the Mexican states of Durango, Sonora, Chihuahua, Coahuila, and Nuevo León. Over almost its entire geographic range, it produces red to scarlet floral bracts, calyces, and corolla margins. There are three named varieties of the species, all red bracted, at the northern and northwestern edges of its range: from Arizona, var. *gloriosa* (Britt.) Cockerell (The Southwest 2:134. 1900.); from Colorado, var. *gracilis* Cockerell (Bull. Torr. Bot. Club 17:35. 1890.); and from New Mexico, var. *intermedia* Cockerell (The Southwest 2:134. 1900.). The taxonomic status of these is not evaluated here, but only the first has generally been recognized in regional floristic treatments. I have, however, examined specimens from over the entire range of *C. integra*.

Warnock (1977, p. 201) noted that "color variation is unusual" in *Castilleja integra* and provided a photograph of a rare variant with yellow bracts from a primarily red bracted population about 10 miles south of Alpine in Brewster Co. I have observed only three collections of such a yellow variant of *C. integra*: (1) *Scott 2* (SRSC) from near Panther Junction in Brewster Co. - *Scott 1*

(SRSC) from the same area is typical red bracted *C. integra*, (2) *Steiger 1212* (NY) from Boot Canyon in the Chisos Mts., and (3) *Stewart 1739* (GH) from the Sierra de la Encantada in northwestern Coahuila, México. The occurrence of these yellow bracted but otherwise typical plants of *C. integra* along the very eastern margin of the species range, facing the geographic ranges of two, yellow bracted, closely related taxa (*C. genevievana* and *C. purpurea* var. *citrina*), seems likely to be indicative of an earlier genetic connection between all three.

Among all of these populations of *Castilleja integra*, one feature in particular appears to indicate their genetic coherence. While most of the hairs of the stems and leaves are unbranched, at least some of them are branched. The basal cell varies in length from ca. 0.02-0.10(-0.40) mm, then branches into two thinner, divergent cells that are also variably elongated and contribute to the lanate appearance of the vestiture. I have not been able to discover a geographic pattern that would predict the relative abundance (branched/unbranched) of the branched hairs, which varies from about 0.1-10.0 percent (or sometimes greater on the leaves). All plants over the entire range of the species produce branched hairs at least at a low frequency.

In trans-Pecos Texas, *Castilleja lanata* is the only other species with branched hairs similar to those of *C. integra*. The former is easily identifiable by the dense, close, white woolly pubescence of its stems and both surfaces of its leaves. All of the hairs are composed of a short stipe with 2-4, elongated lateral branches (up to 2 mm long) produced at the apex of the stipe and that form the mass of the conspicuous vestiture.

Few other American species of *Castilleja* are known to produce branched hairs, among them *C. dendridion* Nesom and *C. galehintoniae* Nesom from México (see Nesom 1992) and *C. pruinosa* Fern. and individuals of *C. applegatei* Fern. var. *fragilis* (Zeile) N. Holmg. of the northwestern United States. Except for *C. dendridion*, the hairs of these taxa are similar to those of *C. integra* and *C. lanata*, but they tend to produce secondary branches. Holmgren (1971) considered the similarity in trichome morphology significant enough to support an hypothesis of introgression between the two northwestern U.S. taxa, which otherwise are relatively distantly related between themselves. It also seems plausible that the branched hairs of *C. integra* indicate a close relationship between it and *C. lanata*. Complicating this hypothesis somewhat is the observation that the rare endemic, *C. organorum* Standley of the Organ Mountains in southeastern New Mexico, also bears a low percentage of branched hairs similar in morphology to those of *C. integra* and *C. lanata*, both of which also occur in the Organ Mountains. The calyx of *C. organorum*, however, is asymmetrically divided, and its evolutionary relationships are probably more closely linked to *C. wootonii* Standley and *C. linariifolia* Benth. (see comments below).

Castilleja lanata and *C. integra* are sympatric over the greatest parts of their geographic ranges. The former has a slightly broader range than the lat-

ter, occurring at lower elevations and further to the south in México. *Castilleja integra* occurs at higher elevations and slightly further to the north (northern New Mexico and southern Colorado), and even in the area where *C. lanata* does not occur, the vestiture of *C. integra* includes branched hairs at least at a low frequency. This may indicate that branched hairs were present in the ancestral populations of *C. integra*, rather than acquired through later hybridization and introgression with *C. lanata*, although the latter processes might account for the variation in abundance of branched hairs in *C. integra*. *Castilleja integra*, however, is more similar to *C. genevievana* and presumably shares with it a more recent common ancestor. *Castilleja lanata* is partially sympatric with *C. genevievana* (Maps 1 and 3) with no evidence of gene flow.

Chromosome numbers have been reported from numerous populations of *Castilleja integra* (Heckard 1958, 1968; Heckard & Chuang 1977; and Ward 1983, 1984). In each of Arizona, Colorado, and New Mexico, both diploids (n=12) and tetraploids (n=24) are known, and Heckard & Chuang (1977, p. 163) noted that "No cytogeographic pattern is apparent in the distribution of the two chromosome levels in this fairly wide-ranging species." Lockwood & Forstner (1991) reported a hexaploid of *C. integra* from near Alpine and a diploid of *C. elongata* from the Chisos Mountains (both from Brewster Co., Texas). Unpublished chromosome counts (as specimen annotations in 1991 by Lockwood at SRSC) indicate that tetraploid populations of *C. integra* also occur in trans-Pecos Texas. The single reported chromosome count of *C. lanata* (Ward 1983) has been diploid.

My interest in the systematics of Texas *Castilleja* was begun without knowledge of another very recent study that included some of the same plants reported on here. I studied the SRSC collections annotated by Mark Lockwood but did not examine his thesis (1991) until after the essential completion of my own manuscript. The strong contrasts in our approaches and conclusions, discussed below, are the result of totally independent studies.

A strong point of disagreement between the present study and Lockwood's (1991) concerns the nature of variability within what can be accepted as *Castilleja integra*. According to Lockwood (p. 86), "The seed-coat similarities between *C. elongata* and [plants from Mt. Livermore in the Davis Mountains identified by the yet unpublished epithet "livermorensis"] also suggest that these two species are very closely related, at least phenetically. This allows for the possibility that they may also represent relictual populations of a once widespread species that has undergone speciation in the isolated montane habitats of the Davis and Chisos Mountains. *Castilleja integra* is also closely related to these two species and possibly shares a common ancestor; ...." In contrast, I suggest that *C. integra* itself is the "once [and still] widespread species" postulated by Lockwood and that some of its relatively high elevation populations are slightly divergent from the morphological form more typical for the species at lower elevations.

Lockwood's key to *Castilleja integra*, *C. elongata*, and "livermorensis" uses only aspects of vestiture and floral bract morphology that I find to be quantitative and intergrading, as discussed above. His data show the calyces and corollas of *C. integra* to be longer than in the other two taxa, where only slight differences in size are shown. In contrast, I did not observe any discontinuous differences in size within what is here recognized as *C. integra* in Texas.

With a more detailed knowledge of the cytogeographical variation, the high elevation forms of *Castilleja integra* in southwestern Texas might indeed prove to be relictual diploids, with intervening areas of the species range primarily filled by polyploids. Diploids of *C. integra*, however, are known to be scattered through a large part of the range outside of Texas. Further, regional differentiation apparently occurs quickly in the genus, as evidenced by numerous narrow endemics and many variable species. Given the wide range of elevations, habitats, and substrates known for *C. integra*, the chromosomal variation, the intergrading morphological variability, some of it possibly reflecting genetic influence of other species, and the proposed but unevaluated varietal taxa already existing within *C. integra*, I can find no satisfactory or appropriate way to recognize segregate taxa, even at the varietal rank, within it from Texas. My view of the taxonomy of this species as it occurs in Texas is summarized below.

Castilleja integra A. Gray *in* Emory, *Rep. U.S. & Mex. Boundary Surv.* 2(1):119. 1858. SYNTYPES: UNITED STATES. Gray cited collections by Wright, Bigelow, Kreuzfeldt, Fendler, and E.K. Smith. The details of the necessary lectotypification will be discussed in a separate paper (Boufford & Nesom in prep.).

Castilleja elongata Pennell, Proc. Acad. Nat. Sci. Philad. 92:306. 1940. TYPE: UNITED STATES. Texas: Brewster Co., wooded slopes of northern Chisos Mountains, ca. 6000 ft, Aug 1934, *T.L. Steiger 1689* (HOLOTYPE: NY!).

Plants perennial. Stems 15-45(-60)(-90 in Brewster Co.) cm tall, lanose to villous, with a mixture of simple and branched hairs, the stipes 0.02-0.08(-0.4) mm long, bearing 2(-4) branches, the simple hairs and branches 0.1-0.5(-0.8) mm long. Leaves 2-6(-8) cm long, linear to narrowly lanceolate, (1-)2-7(-9) cm long, (1-)2-6(-8) mm wide, the lower surfaces densely invested but not obscured by stiff, short, somewhat retrorsely oriented hairs, the longer of these also commonly apically branched. Bracts entire or with 2 lobes originating from middle to near the apex, the apices with capitate glandular hairs. Calyces (18-)21-35(-38) mm long, the primary lobes (7-)10-16(-18) mm long. Corollas (23-)28-42(-47) mm long, the galea (8-)10-17 mm long, the tube 17-27(-30) mm long.

Limestone and igneous substrates; (2800-)3200-8000(-8600) ft; flowering late Mar-Sep(-Oct).

The status of *Castilleja ciliata* Pennell

A population of plants thought to be endemic to the Davis Mountains of Jeff Davis Co., Texas, has been recognized and maintained as *Castilleja ciliata* (Holmgren 1970). Comparative study of these, however, shows them to be conspecific with plants of the Sacramento and White Mountains of southeastern New Mexico, where they are known by the earlier name *C. wootonii*. These are tall perennials with glabrous or very sparsely hairy stems, except in the inflorescence and lowermost portions, which commonly are villous. The linear leaves also range from very sparsely pubescent to completely glabrous or with only short ciliate margins. Those from New Mexico tend to be slightly hairier than the Texas plants, but all are unquestionably the same species. No collections of *C. wootonii* are known from the Guadalupe Mountains, which are in a nearly intermediate geographic position between the Davis and Sacramento Mountains.

The only apparent influence from other species on any of the plants of *Castilleja wootonii* examined in this study is observed in Worthington's collection *12134* (UTEP) from Otero Co., New Mexico. One of the three mounted stems is typical *C. wootonii*; the other two, while nearly identical to the first in overall morphology, have stems sparsely invested with unbranched, retrorsely appressed hairs. The source of this variation is equivocal, but the plants may be hybrids with *C. integra*, which is common in the same area.

Pennell (1940) compared *Castilleja ciliata* to *C. miniata*, but the latter differs in its nearly equally divided calyx (vs. unequally divided in *C. wootonii*). The key provided by Wooton & Standley (1915) contrasted *C. wootonii* with *C. linariifolia*, the latter a widespread species of the western United States and according to Holmgren (1976) a member of subg. *Castilleja*, although it sometimes hybridizes with the relatively more dissimilar *C. miniata* (see notes by Holmgren [1984]). Plants of both *C. linariifolia* and *C. wootonii* produce glabrous or nearly glabrous stems, thick, linear-lanceolate leaves, and unequally divided calyces. Although the former tends to produce more strongly unequal calyx lobes, it is clearly closely related, if not conspecific, with *C. wootonii*. The couplet in Wooton & Standley's treatment compared these two taxa in features of their leaf morphology, but with many specimens of each taxon now at hand, the putative foliar differences appear to be completely overlapping. The following couplet provides an updated comparison of the two taxa.

1. Calyx clefts 10-20(-22) mm deep abaxially and 2-6(-12) mm adaxially, the abaxial clefts 3-5 times longer than the adaxial; bract margins short hispid; lower portion of the stems glabrous to villous. ... *C. linariifolia*

1. Calyx clefts 11-14 mm deep abaxially and 8-9 mm adaxially, the abaxial clefts 1.2-1.8 times longer than the adaxial; bract margins densely long-ciliate; lower portion of the stems villous. ..... *C. wootonii*

Castilleja wootonii Standley, Muhlenb. 5:84. 1909. TYPE: UNITED STATES. New Mexico: [Lincoln Co.,] White Mountains, 7400 ft, 25 Aug 1907, *E.O. Wooton & P.C. Standley 3411* (HOLOTYPE: NY! *ex* NMC, NMC-photo!). In the protologue is additional and conflicting collection data ("Gilmore's ranch on Eagle Creek," at "about 3400 feet"), but it seems reasonable that the NY specimen represents authentic type material.

Castilleja ciliata Pennell, Proc. Acad. Nat. Sci. Philad. 92:306. 1940. TYPE: UNITED STATES. Texas: Jeff Davis Co., Davis Mountains, rocky slopes of Mt. Livermore, 2200 m, 6 Jun 1928, *E.J. Palmer 34383* (HOLOTYPE: PH!; Isotype: NY!). The PH specimen was annotated in an undated, unsigned note as "=*C. wootoni* Standl. *fide* Pennell."

Additional specimens examined: UNITED STATES. New Mexico: Lincoln Co.: White Mts.: Eagle Creek Canyon, ca. 7 mi NW of Ruidoso, locally common on shady aspects of S-facing exposed granite faces, pine-oak-Douglas fir, 11 Jul 1982, *Soreng, Spellenberg, & Ward 2024*, voucher for chromosome count of n=12, reported by Ward 1983 (NMC); N of Sierra Blanca on trail to MonJeau lookout, 8 Sep 1970, *Spellenberg 2392* (NY); White Mt. Peak, 1897, *Wooton s.n.* (NMC) and 1901, *Wooton s.n.* (NMC); ca. 2.0 mi W of Sierra Blanca Ski Lodge, lower part of Apache Bowl Ski Area, open meadows, 11,000 ft, 28 Jun 1980, *Worthington 6148* and *6149* (UTEP); ca. 1.0 air mi W of the Sierra Blanca Ski Resort, bottom of ravine through conifer forest near stream, 10,800 ft, 5 Jul 1981, *Worthington 7227* (UTEP); entrance to Sierra Blanca Ski Area, ca. 9800 ft, 7 Aug 1984, *Worthington 12307* (UTEP). Otero Co.: White Mts.: [no other data], Jun 1936, *Hinckley 1024* (NY,TEX); divide above the Mescalero agency, 1895, *Wooton s.n.* (NMC); Sacramento Mts.: Cloudcroft pine-spruce-aspen, partly open, wooded slopes, 19 Aug 1968, *Correll & Correll 36130* (LL); Mescalero Apache Indian Reservation, Silver Lake, 2450 m, 3 Jul 1979, *Freeman s.n.* (UTEP); S of Cloudcroft, 21.1 mi along State Rd. 24, Cathey Canyon Vista, open grassy area in dry pine forest, 6 Jul 1983, *Hardison 11* (TEX); Cloudcroft, Fir Campground, rocky hillside with pine and fir, 17 Jul 1965, *Iwen 199* (TEX); Sacramento's Silver Campground, 8 Sep 1979, *Patrick s.n.* (UTEP); High Rolls, 19 Oct 1969, *Smartt 43* (UTEP); Cloudcroft, 19 Oct 1969, *Smartt 93* (UTEP); vicinity of Toboggan (an old settlement) ca. 3.5 mi W of Cloudcroft in bottom of canyon, pine-oak-Douglas fir, 10 Aug 1969, *Spellenberg 2081* (NMC); Cloudcroft, 1899, *Wooton s.n.* (NMC); Mescalero reservation, 1905, *Wooton s.n.* (NMC); canyon between entrance to Sunspot and road S down Sacramento Canyon, N slope, limestone

soil, edge of Douglas Fir, 9100 ft. 28 Jul 1979, *Worthington 4793* (UTEP); Bailey Canyon ca. 2 mi NW of Cloudcroft, mixed pine-fir forest, 8400 ft, 1 Aug 1982, *Worthington 8572* (UTEP); upper Russia Canyon ca. 0.2 mi E of Hwy 64, 8900 ft, 24 Jun 1984, *Worthington 12134* (UTEP). Texas: Jeff Davis Co., Davis Mts.: common on Livermore peak and spur ridges, 9-12 Jul 1921, *Ferris & Duncan 2552* (NY); Oct 1937, *Hinckley "985"* (TEX); infrequent in moist canyons at higher elevations, high gorge of Madera Canyon on W slope of Mount Livermore, ca. 2350 m, 26 Jul 1937, *Hinckley 985* (NY-2 sheets); Mt. Livermore, W branch Madera, oak woodland, ca. 2300 m, 27 Aug 1939, *Hinckley s.n.* (GH); Tobe gap, 1/4 mi W of Mt. Livermore peak, 30 Sep 1991, *Lockwood 288* (SRSC); N slope of Mt. Livermore near peak, 30 Sep 1991, *Lockwood 296* (SRSC); Turman Ranch ca. 4 mi SSE of Mt. Livermore at upper end of Merril Canyon, steep N-facing slope in very rocky soil, beneath *Pinus cembroides* and *Quercus gambellii*, 20 Oct 1990, *Lockwood 193* (SRSC); N slope of Mt. Livermore on steep grassy slope in open area, 16 Oct 1990, *Lockwood 188*, voucher for chromosome count of n=12, reported by Lockwood & Forstner 1991 (SRSC); infrequent at upper spring in Madera Canyon, 11 Sep 1947, *Warnock 7460* (SRSC,TEX); 0.8 air mi SE of top of Mt. Livermore, just over N side of crest of mountain, semi-open grassy area, 7800-7900 ft, 2 Sep 1979, *Worthington 5155* (SRSC,TEX,UTEP); 18 Aug 1914, *Young s.n.* (TEX); 16 Sep 1918, *Young s.n.* (TEX).

Pennell's hypothesis that *Castilleja ciliata* is most closely related to *C. miniata* was adopted by Lockwood (1991). Lockwood's claim (p. 70) that his data "show unequivocably that Pennell was correct ..." in this view and his suggestion (p. 86) that "perhaps *C. ciliata* was derived from a relictual population of *C. miniata* ..." are unjustified, because the only taxa of *Castilleja* included in his study were *C. ciliata, C. miniata*, and *C. integra* (including the two trans-Pecos segregates). For the same reason, there is no support for Lockwood's assertion (p. 89) that the flavonoid components of these five taxa show them to be "unequivocally ... closely related, perhaps even at the sectional or other infrageneric level, within the genus." His study of flavonoids, seed coat morphology, and pollen morphology provide positive evidence for placing the plants involved into two groups, *C. ciliata* and *C. miniata* vs. the *C. integra* complex, but no evidence for any other taxonomic conclusions. I have not seen a specimen representing what Lockwood referred to (p. 70) as "possibly a relictual population of *C. miniata*" from Mount Livermore.

IV. The identity of *Castilleja latebracteata* Pennell

Castilleja rigida is the correct name for the plants of trans-Pecos Texas that have been identified as *C. latebracteata* (Holmgren 1970), and most recently as *C. nervata* Eastwood (Johnston 1990; Hatch *et al.* 1990). It is a relatively

common species of the Chihuahuan Desert region in the Mexican states of Durango, Zacatecas, Chihuahua, Coahuila, and Nuevo León (see Nesom 1992 for details). Map 4 shows the distribution of *C. rigida* in Texas, where it is not known to hybridize with any other species.

V. The identity of *Castilleja tortifolia* Pennell

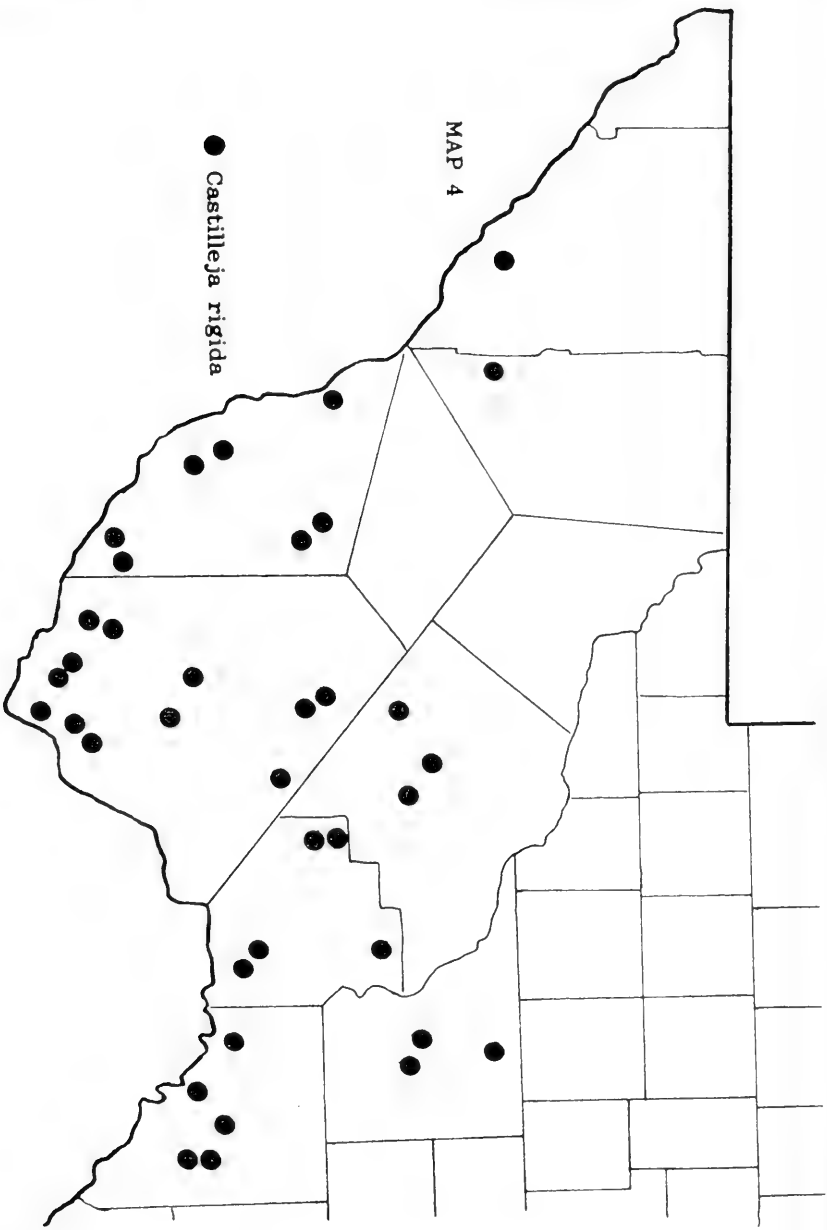
In his discussion following the description of *Castilleja tortifolia*, Pennell noted that it is closely related to *C. mexicana* (Hemsl.) A. Gray, differing in aspects of its leaf morphology and its white (vs. yellow) flowers. With many more specimens now available for study, however, it is clear that only a single species is represented. This was also tentatively surmised by Holmgren (1970) and confirmed by him in 1980, as evidenced by his identification and annotations of specimens in LL,TEX. *Castilleja mexicana* is represented in collections I have studied from the Mexican states of Durango, Chihuahua, Zacatecas, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, and Aguascalientes and from trans-Pecos Texas (Map 5) in Brewster, Culberson, Jeff Davis, and Presidio counties.

Castilleja mexicana (Hemsl.) A. Gray. BASIONYM: *Orthocarpus mexicana* Hemsl., *Biol. Centr.-Amer. Bot.* 2:463, t. 63. 1882. TYPE: MEXICO. Zacatecas: *Coulter s.n.* (HOLOTYPE: K, not seen). *Castilleja mexicana* (Hemsl.) A. Gray, Proc. Amer. Acad. Arts 21:404. 1886.

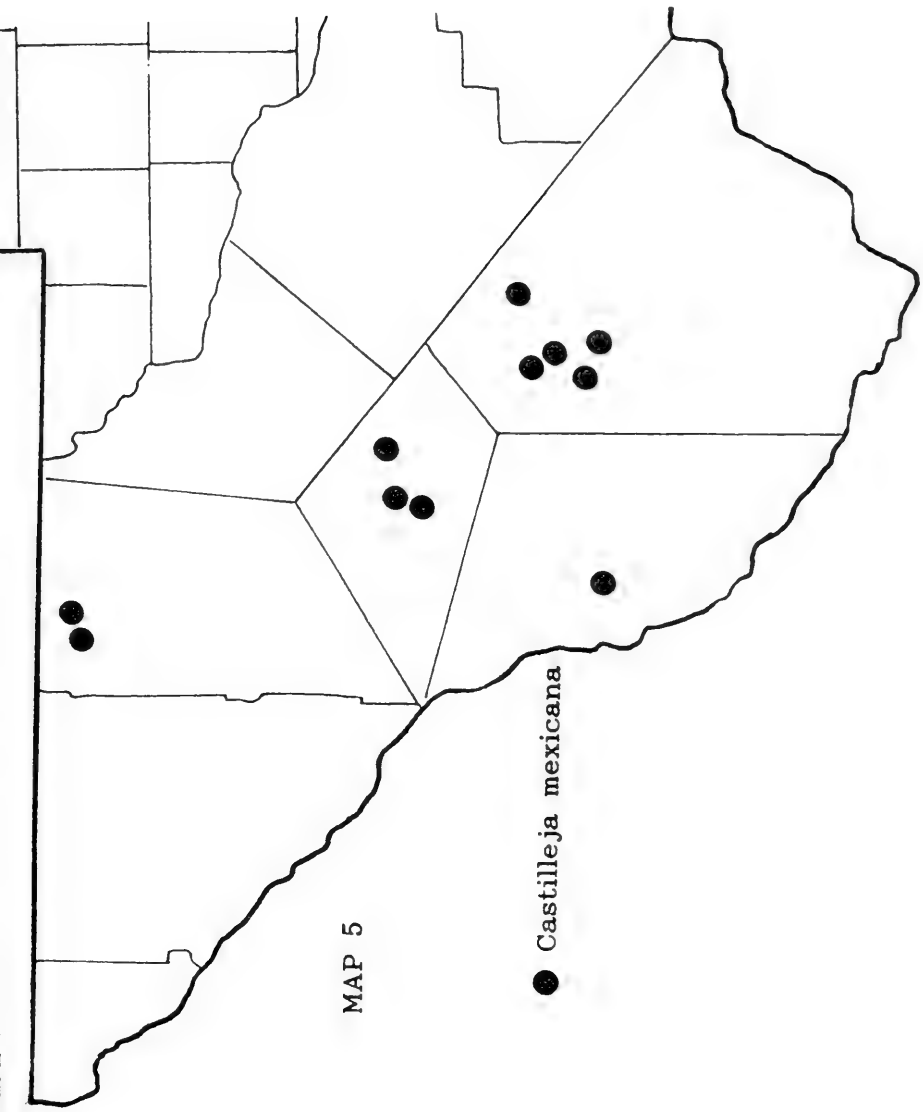
Castilleja tortifolia Pennell, Proc. Acad. Nat. Sci. Philad. 92:304. 1940. TYPE: UNITED STATES. Texas: Jeff Davis Co., Davis Mts., rocky open ground near Livermore Peak, 2500 m, 14 Jun 1926, *E.J. Palmer 30867* (HOLOTYPE: PH!).

Castilleja mexicana is sometimes confused with *C. sessiliflora* Pursh, the latter of which is by far the more abundant and widespread species in Texas (Map 6) and which occurs from southeastern Canada southward primarily through the Great Plains to Illinois and Missouri, Colorado, Arizona, and Texas, and the Mexican states of Coahuila and Nuevo León. Both species are distinctive in their falcate corollas long exserted from the calyx, but they can be easily distinguished by reference to the following comparison.

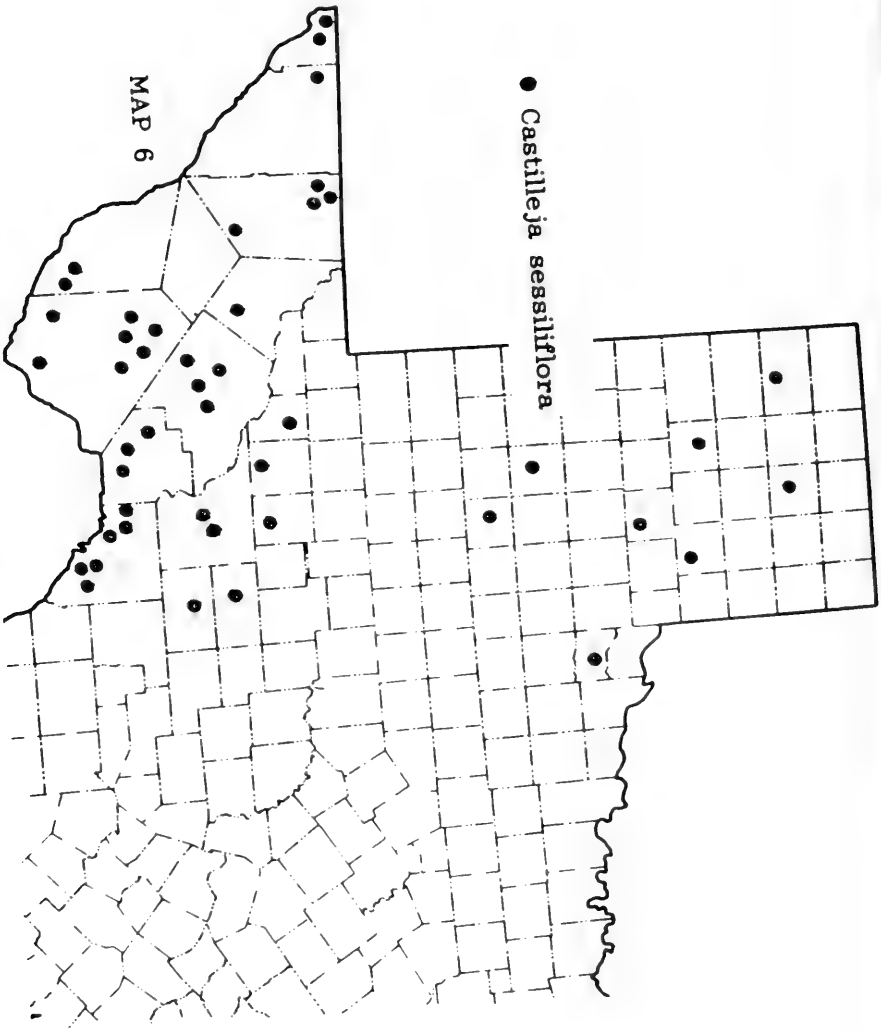
1. Plants annual or short lived perennials from a woody but slender taproot; bracts yellow; stems with a mixture of stiffly spreading nonglandular and gland tipped hairs; primarily igneous substrates, 4300-6600 ft in Texas, flowering late Mar-Jul(-Sep). ..... *C. mexicana*



Map 4. Distribution of *Castilleja rigida* in Texas.



Map 5. Distribution of *Castilleja mexicana* in Texas.



Map 6. Distribution of *Castilleja sessiliflora* in Texas.

1. Plants perennials from a woody, distinctly thickened root; bracts pink to yellow; stems nearly lanose with long, somewhat intertwined, nonglandular hairs; limestone and gypsum substrates, (950-)2100-5400 ft in Texas; flowering Mar-Jul(-Oct). ..... *C. sessiliflora*

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NEW SPECIES AND TAXONOMIC EVALUATIONS OF MEXICAN *CASTILLEJA* (SCROPHULARIACEAE)

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ABSTRACT

Four new species of *Castilleja* are described from México. **Castilleja jiquilpana** from Michoacán is most closely related to *C. scorzoneraefolia*. **Castilleja durangensis** from Durango is most closely related to *C. aspera*, and **C. galehintoniae** from Nuevo León is most closely related to *C. lanata*. **Castilleja dendridion** from Oaxaca has much more uncertain evolutionary affinities. The identities and taxonomic status of the accepted species *C. scorzoneraefolia*, *C. falcata*, *C. rigida*, *C. nervata*, *C. bella*, and *C. aspera*, as well as taxa relegated to synonymy, are evaluated.

KEY WORDS: *Castilleja*, Scrophulariaceae, México

In the course of providing general identifications of recent collections of *Castilleja* from northern México, as well as curating LL,TEX collections of the genus, a number of taxonomic problems and undescribed taxa have come to light. A review of the genus in México and Central America (Nesom unpublished) accounts for 52 species in mainland México, an additional thirteen in Baja California (only one of these occurs on the mainland), and nine in Central America (six endemic there). Eastwood's study (1909) of Mexican and Central American *Castilleja* recognized 54 species, seventeen originally described by her. Brandegee (1914) described an additional species from mainland México, Standley & Steyermark (1944) one from Guatemala, Standley (1936; 1940) three species from mainland México and one (1938) from Costa Rica, the latter including three species later proposed by Pennell, Crosswhite (1970) one, Rzedowski (1975) one, Holmgren four from México (1976) and four from Costa Rica and Panamá (1978), and Moran (*in* Levin & Moran 1989) one from México. Breedlove & Heckard (1970) placed a new species from Sinaloa in the monotypic genus *Gentrya*, which has recently been positioned within

Castilleja (Chuang & Heckard 1991). Six other species have been described since 1909 from Baja California or from southern California and are known to occur in Baja California. The present study adds four new species of *Castilleja* from mainland México; a companion paper (Nesom 1992) adds another that is primarily centered in Texas but that also occurs in Coahuila.

Where species have been problematic in their past circumscriptions, their identity and geographical distribution are documented by specimen citations in the present study. All taxa are mapped, based primarily on specimens from GH,MO,NY, and LL,TEX.

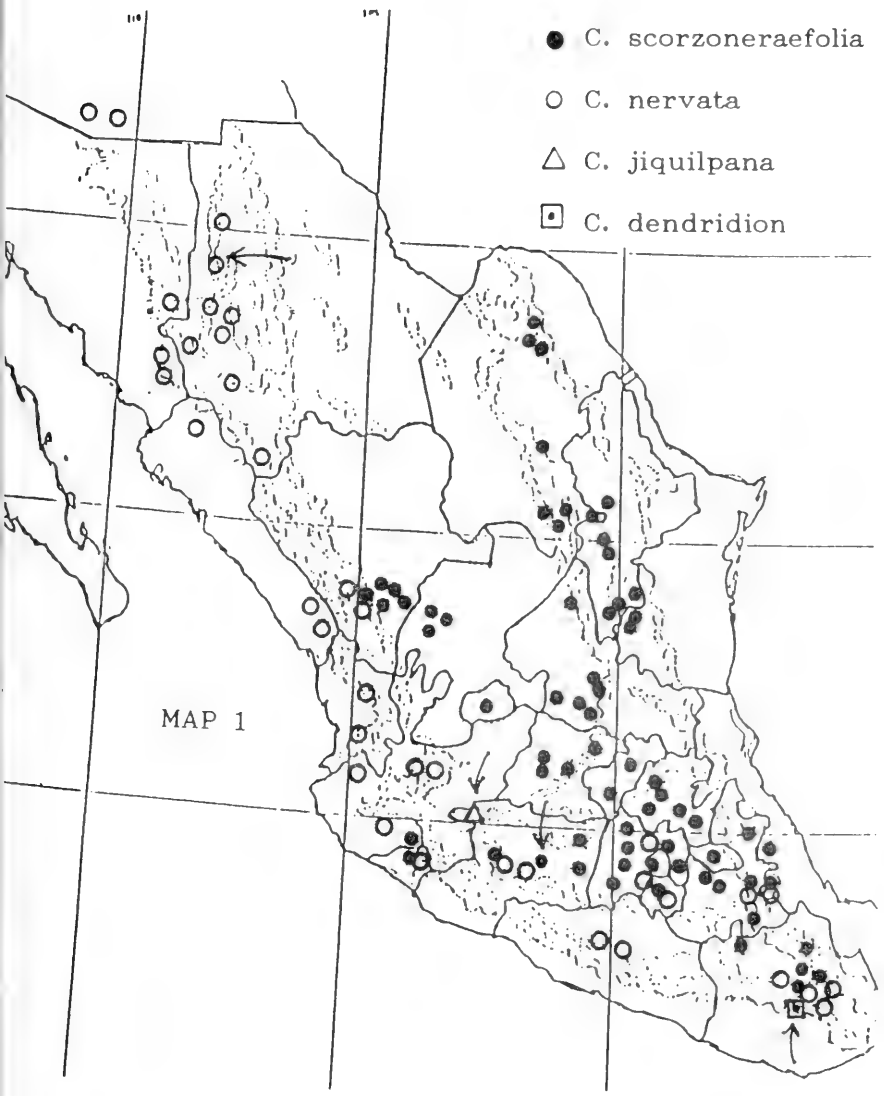
I. The identity of *Castilleja scorzoneraefolia* Kunth

Castilleja scorzoneraefolia Kunth, *Nov. Gen. & Sp.* 2 [folio]:267. 1818; 2 [quarto]:331, tab. 165. 1820. TYPE: MEXICO. Michoacán: "Ario Pazcuaro" (as on the specimen), [Sep 1803], *Humboldt & Bonpland s.n.* (HOLOTYPE: P fiche!). The protologue: "Crescit in rupestris Novae Hispaniae prope Pazcuaro et Ario, alt 1100 hex. 4 Floret Augusto."

Castilleja lithospermoides Kunth, *Nov. Gen. & Sp.* 2 [folio]:266. 1818; 2 [quarto]:331, tab. 164. 1820. TYPE: MEXICO. Hidalgo: "Moran" (as on the specimen), [May-Jun 1803], *Humboldt & Bonpland s.n.* (P fiche!). The protologue: "Crescit in temperatis Novae Hispaniae prope Real del Monte et Moran, et in Regno Quitense prope Chillo, alt 1350 hex. 4 Floret Majo-Junio." The sheet of *C. lithospermoides* has 3 branches: the one on the left is typical *C. scorzoneraefolia*; the identity of the other two is more equivocal, and it is possible that they might even represent what is identified in the current study as *C. nervata* Eastwood. If so, however, it is not likely that they originated from central Hidalgo, which is north of the range of *C. nervata* (Map 1). Further, the original illustration of *C. lithospermoides* (tab. 164) shows a plant nearly identical to that pictured for *C. scorzoneraefolia* (tab. 165), the leaves with expanded and distinctly clasping bases and corollas exserted from calyces.

Castilleja glandulosa Greenm., Proc. Amer. Acad. Arts 41:247. 1905. TYPE: MEXICO. México: hills near Lecheria Station, 2200 m, 2 Jul 1904, *C.G. Pringle 10,000* (HOLOTYPE: GH!; Isotypes: LL!, MO!).

Perennials usually from a taproot. Stems herbaceous, 10-30(-40) cm tall, erect, straight, commonly with short, eglandular, deflexed hairs, stipitate glandular hairs, and much longer, stiffly spreading, eglandular hairs; lower leaf surfaces moderately to densely hirsute with stiff, straight, eglandular hairs,



Map 1. Distribution of *Castilleja nervata*, *C. scorzoneraefolia*, *C. jiquilpana*, and *C. dendridion*. Arrows show the locations of type collections.

sometimes also with glandular hairs, the margins commonly ciliate with much longer hairs. Leaves 2-7 cm long, narrowly triangular, entire, 3 veined, the veins sometimes prominently raised, sessile, distinctly clasping. Floral bracts 24-30 mm long, oblong lanceolate to obovate, 3 veined, 5-12 mm wide, entire, the upper red tipped. Calyx red and glandular at the apex, 19-32 mm long, from the base is somewhat constricted at ca. midlength, then broadening again toward the apex, equally divided, the primary lobes 7-12 mm long, the secondary lobes rounded and shallow, 1-3 mm long, sometimes completely absent. Corolla 21-37 mm long, the lower lip of 3(-5), thick green teeth 1-2 mm long, the galea 7-12 mm long, 30%-34% as long as the corolla, usually exserted from the calyx 3-9 mm, rarely included. Chromosome numbers, n=12 and n=24, both unpublished counts by Chuang, according to label data.

Widespread in temperate areas of southcentral to northeastern México (Map 1); (950-)1250-3590(-4100) m; Apr-Sep.

Castilleja scorzoneraefolia is one of the most common and widespread species of México. It is somewhat variable in features of vestiture, calyx morphology, and degree of corolla exsertion, but for the most part, identifications of this species are relatively consistent. Possible intermediacy between *C. scorzoneraefolia* and *C. rigida* Eastwood and *C. nervata* is discussed below. Numerous collections from westcentral Zacatecas and adjacent Durango appear to represent a disjunct, northwesternmost segment (Map 1) of *C. scorzoneraefolia* and may prove to deserve taxonomic recognition. These plants consistently produce highly glandular stems and leaves, leaves with sinuate margins, prominent axillary clusters of leaves, and calyces with red and white longitudinal stripes. Such features, however, also occur in plants scattered through the range of the species.

Eastwood (1909) distinguished *Castilleja scorzoneraefolia* from close relatives by its lower corolla lip of five teeth, three primary ones and two smaller ones in the sinuses of the others. I also have observed this feature, but it is not constant within the species. A similar lower corolla lip also occurs sporadically in plants of *C. rigida* (see below).

Plants with 3 lobed bracts and leaves, but otherwise mostly similar to *C. scorzoneraefolia*, occur in the high elevation regions of Veracruz (Orizaba and Perote, Map 1), where they have been named as *C. falcata* Eastwood. These apparently are annual or short lived perennials and are erect and single stemmed from the base. They appear to intergrade with typical *C. scorzoneraefolia*, but no other plants of the latter over the range of the species produce this morphology and *C. falcata* is tentatively maintained here as a taxon deserving recognition at least at some rank.

Castilleja falcata Eastwood, Proc. Amer. Acad. Arts 44:575. 1909. TYPE: MEXICO. Puebla: Mount Orizaba, 3660 m, 14 Aug 1901, *C.G. Pringle*

8560 (HOLOTYPE: GH!; Isotype: MO!).

In contrast to the somewhat ambiguous distinction of *Castilleja falcata* from *C. scorzoneraefolia*, another closely related but previously unrecognized population system appears to be clearly distinct as a species and is formally described here.

Castilleja jiquilpana Nesom, *sp. nov.* TYPE: MEXICO. Michoacán, 1 mi W of El Fresno, 6 mi from jct of Hwy 15 on Hwy 110, 6000 ft, 7 Jul 1966, *E. Molseed 441* (HOLOTYPE: LL!; Isotypes: MO!,UC).

Castillejae scorzoneraefoliae Kunth similis sed duratione breviore, caulium vestimento sparsim piloso eglanduloso, foliorum lobis linearibus, et calycibus flavifasciatis differt.

Plants apparently annual, from a short, slender taproot. Stems 22-38 cm tall, eglandular, very sparsely pilose with vitreous, spreading hairs mostly 0.5-1.0 mm long and a sparse understory of much smaller, loose, often somewhat deflexed hairs. Leaves subclasping, lanceolate, 2-5 cm long, 2-7 mm wide (at midleaf), 3 veined with the midvein raised, at least the lower leaves with 1-3 pairs of filiform lobes from the upper half of the broad central portion of the lamina, upper leaves entire to lobed. Mature inflorescence/infructescence 8-15 mm long; floral bracts lanceolate, the lowermost sometimes lobed like the leaves, 17-25 mm long, 4-6 mm wide, the upper third red and minutely glandular. Calyx red tipped and glandular at the apex, 15-17 mm long, from the base is somewhat constricted at ca. midlength, then broadening again toward the apex, the primary lobes 6-8 mm long, nearly equal in length, rounded at the apex with barely if at all developed secondary lobes, or shallowly notched with small but distinct secondary lobes, red on the upper fourth, green below, a yellow band ca. 1 mm wide between the red and green portions. Corolla exserted from the calyx 1-4 mm, the lower lip of 3, thick, green teeth ca. 1 mm long, the galea 6-8 mm long, 33%-45% as long as the corolla, glandular and sparsely pilose. Chromosome number, n=12 (see voucher below).

Northwest Michoacán (Map 1); wet, grassy fields and roadsides, 2050-2310 m; Jun-Aug.

Additional collections examined: MEXICO. Michoacán: Ca. 22 km W of Jiquilpán on Rta. 110, 3 Aug 1966, *Cruden 1149*, voucher for chromosome count of n=12, as *Castilleja glandulosa* [Heckard 1968] (TEX); 12-13 km W of Jiquilpán on Rta. 110, 1 Jul 1968, *Cruden 1322* (NY).

Castilleja jiquilpana apparently is a narrow endemic (Map 1) in a distinctive habitat. All three collections studied were made within about 30 kilometers of each other in the area of Jiquilpán, Michoacán. The plants are similar to *C. scorzoneraefolia* particularly in their subclasping leaves and features of

the calyx. The new species is morphologically distinct in its apparently annual duration (judging from the short, very slender taproot), yellow banded calyces, eglandular and sparsely pilose stems, and deeply divided leaves with linear lobes. Scattered plants of *C. scorzoneraefolia* throughout its range may show some of these features, but the only other plants within the *C. scorzoneraefolia* group with similarly divided leaves and bracts are those of *C. falcata*, *C. moranensis* Kunth, and *C. bella* Standley (see discussion below of the latter two).

Castilleja jiquilpana also is at least superficially similar to *C. saltensis* Eastwood, which is endemic to southeastern Durango. Plants of the latter, however, are shorter with floral bracts that are most often lobed (vs. entire), a more villous stem vestiture of hairs with a strong tendency to be produced in vertical lines, and calyces that lack a yellow band beneath the distal red portion.

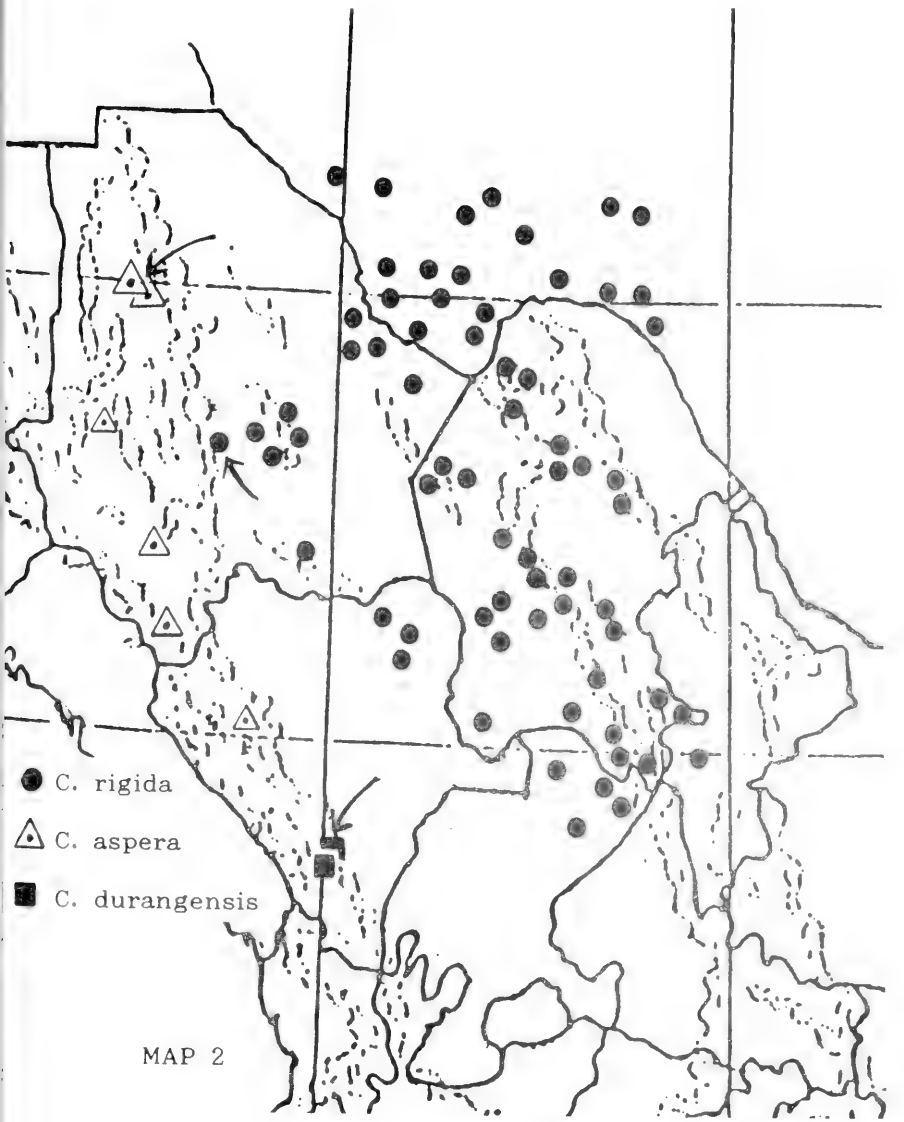
II. The identity of *Castilleja rigida* and *C. nervata*

Castilleja rigida Eastwood, Proc. Amer. Acad. Arts 44:575. 1909. TYPE: MEXICO. Chihuahua: hills near Chihuahua, 16 Apr 1885, *C.G. Pringle 188* (HOLOTYPE: GH!).

Castilleja latebracteata Pennell, Proc. Acad. Nat. Sci. Philad. 73:533. 1921. TYPE: UNITED STATES. Texas: Val Verde Co., High Bridge [Southern Pacific Railroad] of the Pecos, 1000 ft, 27-28 Apr 1903, *Dr. H.A. Pilsbry s.n.* (HOLOTYPE: PH!).

Stems woody, (15-)14-55 cm tall, commonly slightly zig-zag at the nodes. Stem and leaf surfaces softly pilose to villous with eglandular, vitreous, loosely spreading, and somewhat crinkled hairs, mixed with gland tipped hairs. Leaves obovate, sessile, not clasping, without prominently raised veins. Floral bracts entire, 3 veined, 8-16 mm wide. Calyx red tipped and glandular at the apex, 20-32(-36) mm long, from the base is somewhat constricted at ca. midlength, then broadening again toward the apex, the primary lobes lobes (5-)7-12 mm long, nearly equal in length, with rounded, barely developed secondary lobes. Corolla conspicuously exserted from the calyx, (24-)28-36(-42) mm long, the lower lip of 3(-5), thick, green teeth 0.5-1.5 mm long, the galea (8-)10-14 mm long, 33%-45% as long as the corolla. Chromosome number unknown.

Chihuahuan Desert region of Chihuahua, Durango, Zacatecas, Coahuila, and Nuevo León, México, also trans-Pecos Texas (Map 2); matorral, sometimes into mesquite or oak woods, limestone substrates, except in the igneous Santa Rosa Mountains southwest of Muzquiz; (500-)1100-2800 m; (Mar-)Apr-Oct (-Feb).



Map 2. Distribution of *Castilleja rigida*, *C. aspera*, and *C. durangensis*. Arrows show the locations of type collections.

Castilleja rigida is the earliest and correct name for the plants of trans-Pecos Texas and northern México that previously (Holmgren 1970) have been identified as *C. latebracteata* Pennell. The species is almost completely confined to the Chihuahuan Desert Region and occurs relatively abundantly in the Mexican states of Durango, Zacatecas, Chihuahua, Coahuila, and Nuevo León, as well as in southern Texas (Map 2; also see Nesom 1992). The plants are easily identified by their morphology and geographic range and I have not cited specimens.

In its calyx and corolla morphology, *Castilleja rigida* is similar to *C. scorzoneraefolia*, and the two species are almost certainly closely related. There is some indication that gene flow occurs between them where they are sympatric in Coahuila. For example, in the Sierra de la Gavia (35 mi south of Monclova), Henrickson has collected plants of *C. rigida* (oak woods at 4500 ft, *11777b*, NY-2 sheets) with tall, slightly zig-zag stems and nonclasping leaves but atypical in their very narrow floral bracts, in close proximity to *C. scorzoneraefolia* (oak chaparral at 5900 ft, *11808*, NY-2 sheets) with clasping leaves but tall, distinctly woody stems and wide floral bracts. Similar examples can also be found in the region of Muzquiz, Coahuila, at the northernmost extension of the range of *C. scorzoneraefolia*.

Castilleja rigida also has been confused with *C. nervata* Eastwood (in specimen annotations, by my own and those of others, the two species considered together as *C. nervata*). Plants of both species are strongly perennial with woody, slightly zig-zag stems and non-clasping leaves, but they are distinct from each other in both geography (Maps 1 and 2) and a number of morphological features. Both *C. rigida* and *C. nervata* are closely related to *C. scorzoneraefolia*. The three species are distinguished by features in the following couplet.

1. Plants usually with a distinct taproot; stems straight, herbaceous from the base; leaf bases expanded, clasping to subclasping; calyx red tipped; corollas exserted from the calyx. ..... *C. scorzoneraefolia*

1. Plants usually with woody roots but not distinctly taprooted; stems slightly zig-zag at the nodes, basally herbaceous to woody; leaves attenuate to a nonclasping base; calyx red tipped or completely green; corollas included within the calyx or exserted. .....(2)

   2. Corollas (24-)28-36(-42) cm long, exserted from the calyx, the lower lip of linear-attenuate teeth; calyx red tipped; leaves with primary abaxial foliar veins not prominently raised; stem and leaf surfaces softly pilose to villous with eglandular, loosely spreading, and somewhat crinkled hairs, mixed with gland tipped hairs, the leaf margins essentially eciliate. ..... *C. rigida*

2. Corollas 15-24 cm long, completely included within the calyx, the lower lip of deltate or triangular teeth; calyx completely green; primary abaxial foliar veins prominently raised; stems commonly with short, eglandular, deflexed hairs, stipitate glandular hairs, and much longer, stiffly spreading, eglandular hairs, the lower leaf surfaces moderately to densely hirsute with stiff, straight, eglandular hairs, sometimes also with glandular hairs, the margins commonly ciliate with much longer eglandular hairs. ..... *C. nervata*

Castilleja nervata Eastwood, Proc. Amer. Acad. Arts 44:574. 1909. [22 May] TYPE: MEXICO. Chihuahua: vicinity of Madera, 2250 m, May-Jun 1908, *E. Palmer 274* (HOLOTYPE: GH!; Isotype: MO!).

Castilleja angustifolia Mart. & Gal., Bull. Acad. Roy. Sci. Brux. 12(2):29. 1845. TYPE: not seen. Not *Castilleja angustifolia* G. Don, *Gen. Syst. Gard. Bot.* 4:616. 1838, from North America; not *Castilleja angustifolia* (Nutt.) A. Gray *in* Torrey, *Bot. U.S. & Mex. Bound. Surv.* 2(1):118, 1838, from North America. The identity of *C. angustifolia* Mart. & Gal. is accepted here *fide* Eastwood (1909), who noted that it is the same species as *C. lithospermoides* (=*C. nervata* in the sense of the present treatment, see comments below). The name upon which Gray's combination was based, *Euchroma angustifolia* Nutt., almost certainly represents some other species, perhaps *C. angustifolia* (Nutt.) G. Don, rather than the specimen Gray referred to, which was apparently at hand (=*Castilleja integra* A. Gray, a Wright collection from Texas).

Castilleja cryptandra Eastwood, Proc. Amer. Acad. Arts 44:578. 1909. TYPE: MEXICO. Colima: Cuchilla, NE side of Volcán Colima, 22 Jul 1905, *P. Goldsmith 76* (HOLOTYPE: GH!; Isotype: MO!).

Castilleja cruenta Standley, Muhlenbergia 5:82. 1909 [7 July]. TYPE: UNITED STATES. Arizona: Cochise Co., Chiricahua Mountains, rocky spur N of Wilgus Ranch, rhyolite, 6000 ft, 2 Sep 1907, *J.C. Blumer 2133* (HOLOTYPE: NY! *ex* NMC). The identity of these plants with *Castilleja nervata* has also been recognized by N. Holmgren, as evidenced by his 1983 annotation of the type specimen.

Stems woody, (15-)30-100 cm tall, commonly slightly zig-zag at the nodes. Stems commonly with short, eglandular, deflexed hairs, stipitate glandular hairs, and much longer, stiffly spreading, eglandular hairs; lower leaf surfaces moderately to densely hirsute with stiff, straight, eglandular hairs, sometimes also with glandular hairs, the margins commonly ciliate with much longer

hairs. Leaves obovate to linear lanceolate, sessile, not clasping, the 3 major veins prominently raised on the lower surface. Floral bracts entire, 3 veined, 6-15 mm wide. Calyx green, 15-24 mm long, tubular, the primary lobes 8-14 mm long, nearly equal in length, with rounded, barely developed secondary lobes. Corolla completely included within the calyx, 15-24 mm long, the lower lip of 3, green, thickened, linear-attenuate teeth 2.0-2.5 mm long, the galea 5-8 mm long, ca. 33% as long as the corolla. Chromosome numbers, n=12, n=24 (see vouchers below).

Southern Arizona in the United States, and in the following Mexican states: Sonora, Chihuahua, Distrito Federal, Sinaloa, Durango, Nayarit, Jalisco, Colima, México, Michoacán, Guerrero, Morelos, Puebla, Veracruz, and Oaxaca (Map 1); rocky slopes or openings, oak to pine-oak or pine woods, rarely in pine-fir; 750-2300(-2600) m; (Apr-)Jul-Oct(-Nov). Eastwood (1909) noted that this species (as *Castilleja lithospermoides*, see comments below) occurs in South America, but I have confirmed its presence only in México.

Representative collections examined: MEXICO. Chihuahua: Mpio. Batopilas, N of Quirare on La Bufa-Creel road, 31 Jul 1977, *Bye 7782* (GH); Mesa de Arroyo Seco, 25-30 km SW of Minaca, 16-17 Sep 1934, *Pennell 18846* (GH,NY). Distrito Federal: Lomas, Sep 1930, *Lyonnet 743* (MO). Durango: Along trail from Pueblo Nuevo to Cueva, 30-31 Aug 1934, *Pennell 18487* (GH). Guerrero: SW of Xochipala, ca. 40.5 km SW of K236 on Rta. 95, 20 Jul 1969, *Cruden 1628* (NY). Jalisco: Ca. 17.5 km S of Autlán on Route 80, 2 Aug 1969, *Cruden 1672* (NY); hills near Guadalajara, 13 May 1901, *Pringle 9461* (GH,NY). México: 10 mi N of México City near Atzcapotzolco, 1-15 Jul 1937, *Happ 109* (MO). Michoacán: Cerro Tancitaro, 19 Aug 1940, *Leavenworth 664* (NY, with *Castilleja scorzoneraefolia*); hills near Patzcuaro, 30 Jul 1892, *Pringle 4168* (GH,MO,NY). Morelos: Cuautla, Jul 1930, *Lyonnet 743* (NY); La Herradura near Cuernavaca, 14 May 1938, *Williams 3048* (MO). Nayarit: Cerro de San Juan, SW of Tepic, 18 Aug 1935, *Pennell 19754* (GH,NY); ca. 19 km S of Tepic, 27 Jun 1968, *Cruden 1313* (NY). Oaxaca: Dpt. Mixe, between San Isabel and San Juan Mazatlán, [no date], *Lipp 37* (NY); Dept. Etla, 17 km NE of San Gabriel Etla, 13 May 1985, *López G. 258* (NY). Puebla (?): Orizaba, Engenio, Sierra de Cruz, Aug 1853, *Muller s.n.* (NY). Sinaloa: Cerro de la Sandia, NE of Panuco, 29-30 Aug 1935, *Pennell 20050* (GH). Sonora: Puerta de Pinitos, 14 Oct 1890, *Hartman 150* (GH); Bakachaka, Río Mayo, 5 Jul 1935, *Gentry 1464* (GH,MO); ridge S of Arroyo Gochico, E of San Bernardo, 5-9 Aug 1935, *Pennell 19531* (GH,NY). Veracruz: Mt. Orizaba, Mageyas to Lomogrande, 26 Apr 1938, *Balls 4347* (GH).

UNITED STATES. Arizona: Santa Cruz Co., Santa Rita Mountains, 7000 ft, 25 Jul 1884, *Pringle 8175* (NY) and *8174* (NY).

Eastwood (1909) recognized *Castilleja nervata* only from Chihuahua. The remainder of the species (as treated here) was identified by her as *C. lithospermoides*, although she noted that the two taxa were similar. The type of *C.*

lithospermoides, however, was collected in Hidalgo (north of the known range of *C. nervata*), and the type specimen (fiche) as well as the original illustration show clasping leaves and exserted corollas characteristic of *C. scorzoneraefolia*. Jiménez (1985) clearly used *C. lithospermoides* as the name for what is identified in the current study as *C. scorzoneraefolia*; the plants he identified as *C. scorzoneraefolia*, with acute calyx lobes and large anthers, are some other species.

The type of *Castilleja cruenta* (Chiricahua Mountains, Arizona), is typical of *C. nervata*; the plants from the Santa Rita Mountains, Arizona (*Pringle 8174* and *8175*), are atypical in their shallowly toothed floral bracts but otherwise so similar to *C. nervata* that they must be referred to it.

Castilleja nervata and *C. scorzoneraefolia* have closely contiguous geographic distributions (Map 1), and apparent intermediates may be found along the area where their ranges abut. The two species are sympatric in the area of Edo. México, Morelos, the north half of Oaxaca, and Puebla, the area of Volcán de Colima along the Jalisco-Colima border, the area of Mt. Tancitaro, Michoacán, and in southwestern Durango. Within *C. scorzoneraefolia*, scattered through its range, aspects of variability support an hypothesis of close relationship to *C. nervata*. Although the corollas are usually well exserted in *C. scorzoneraefolia*, they are sometimes nearly included, and although the vestiture is mostly of loose hairs, they may be distinctly hispid.

III. The identity of *Castilleja bella*

Castilleja bella has previously been known to occur on Cerro Potosí, Nuevo León (the type locality) and Cerro Peña Nevada (along the Nuevo León-Tamaulipas border) (McDonald 1990), and its presence is here recognized on the high peaks east of Saltillo, Coahuila (Sierra Coahuilón and Sierra La Marta). The extension of its known range to the latter area makes its distribution more typical of the majority of species of the alpine-subalpine flora of northeastern México (McDonald in press).

Castilleja bella Standley, Field Mus. Pub. Bot. 22:106. 1940. TYPE: MEXICO. Nuevo León: Mpio. Galeana, peak of Cerro Potosí, abundant in meadows above and below timber line, 21 Jul 1935, *C.H. Mueller 2249* (HOLOTYPE: F; Isotype: MO!).

Caespitose perennials from a thick, straight taproot. Stems herbaceous, 2-6(-30) cm tall, stems and leaves very sparsely pilose with loose, vitreous hairs mostly 0.8-1.6 mm long, eglandular. Leaves 2-5 cm long, narrowly triangular, 3 veined, sessile, distinctly clasping, with 1-2 pairs of narrow lobes or the taller plants with at least the lower leaves entire. Floral bracts 23-28 mm

long, oblong lanceolate to obovate, 3 veined, 3-5 mm wide, with 1-2 pairs of narrow lobes, the upper 2/3 of each lobe red tipped. Calyx red and glandular at the apex, 28-36 mm long, equally divided, the primary lobes 6-10 mm long, the secondary lobes rounded and shallow, 1-2 mm long, sometimes completely absent. Corolla 28-38 mm long, the lower lip of 3, fleshy, green teeth 0.5-2.0 mm long, the galea 6-9 mm long, 25%-33% as long as the corolla, exserted from the calyx 1-6 mm. Chromosome number unknown.

High sierra of southeastern Coahuila (Sierra La Marta and Sierra Coahuilón), northcentral Nuevo León (Cerro Potosí), and southern Nuevo León and adjacent Tamaulipas (Cerro Peña Nevada) (Map 4), alpine and subalpine zones, 3000-3700 m; May-Jul(-Nov); at the crests of Sierra La Marta and Sierra Coahuilón among *Pinus culminicola* Andresen & Beaman and shrubs, pine-fir meadows, pine-oak woods, 3016-3600 m; on Cerro Potosí in rocky, alpine meadows and edge of krumholz near the peak, into pine meadows below, 3350-3700 m; on Peña Nevada in the area of the highest peak, 3400-3600 m.

Additional collections examined: MEXICO. Coahuila: Mpio. Arteaga: Sierra Coahuilón, 17 Jun 1991, *Hinton et al. 20998* (TEX); Sierra la Marta, 17 May 1981, *Poole 2316* (TEX); Sierra la Marta, first peak E of Cerro Morro, 20 Jul 1985, *McDonald 1685* (TEX). Nuevo León: Mpio. Dr. Arroyo, Sierra de Peña Nevada: north of Picacho de San Onofre, burned zone on W side, with dominant *Ceanothus* and *Arctostaphylos*, ca. 3400 m, 30 Nov 1984, *McDonald & Gómez 1292* (TEX); Picacho de San Onofre, E side, ca. 3600 m, 5 Jul 1985, *McDonald 1664* (TEX); Mpio. Galeana, Cerro Potosí: NE summit, 13 Sep 1960, *Beaman 4456* (GH); near summit, 27 Aug 1987, *Bogler & Atkins 162* (TEX); summit, 18 May 1982, *Dorr 2277* (TEX); top, 28 Oct 1982, *Grimes 2371* (TEX); Cerro Potosí ascent, 3350 m, 2 May 1969, *Hinton et al. 17012* (TEX); [near summit], 21 Jun 1969, *Hinton et al. 17109* (TEX); summit, 25 May 1969, *Hinton 17049* (TEX); top, 23 Aug 1984, *Lavin 4781* (TEX); alpine zone, 26 Oct 1984, *McDonald & Gómez 1260* (TEX); alpine zone, 26 Jul 1985, *McDonald 1788* (TEX); ascent of Sierra Potosí by the N hogback, abundant on the meadow at the peak and common in the forest immediately beneath, 26 Jul 1934, *Mueller 1234* (GH,TEX); ascent of Sierra Potosí by the north hogback, common in all parts of the pine forest, 26 Jul 1934, *Mueller & Mueller 1239* (GH,TEX); peak, 18 Jul 1938, *Univ. Illinois Exped. 935* (GH,MO); summit, 20 Oct 1979, *Warnock 2013* (TEX); summit, 24 Jul 1977, *Wells & Nesom 235* (TEX). Tamaulipas: Mpio. Miquihuana, Cerro Peña Nevada, 1 Jun 1974, *Patterson 1514* (TEX).

In the original description of *Castilleja bella*, Standley (1940, p. 106) quoted comments by the collector of the paratype regarding variation in the species: "A very conspicuous plant, abundant on the treeless peak, and extending down (equally abundant) into the pine forest and in grassy openings for over 300 meters. In exposed places only 2.5-5 cm high. In the shelter of the timber at times reaching a height of 12 cm, but even in such places most of the plants are

low." The same variation in habit noted by Standley is confirmed by study of the numerous herbarium specimens by which this species is now represented. The plants are mostly acaulescent (2-6 cm tall) in alpine zones, but even on the peak (and near it) of Cerro Potosí, among acaulescent plants are individuals with stems commonly to 12 cm tall and ranging up to 30 cm (e.g., *Hinton 17109, Mueller 1234, McDonald 1788, Bogler & Atkins 162*). Plants with the typical, acaulescent habit occur on Cerro Potosí and Peña Nevada, but so far only taller plants have been collected from Coahuila.

Castilleja bella differs from *C. scorzoneraefolia* in its high elevation habitats, caespitose habit, with numerous branches arising immediately from a thick taproot, floral bracts (and sometimes upper leaves) with 1-2 pairs of narrowly lanceolate lobes, and sparsely villous, eglandular stems. The caespitose habit, however, as well as the reduced vestiture and similar taproots, are also found in some plants of *C. scorzoneraefolia* from Nuevo León and Coahuila, particularly at the upper range of elevation of that species. The primary distinction between *C. scorzoneraefolia* and the taller plants of *C. bella* is the lobing of the floral bracts and upper leaves. In Coahuila and Nuevo León, *C. scorzoneraefolia* occurs at 970-2700 meters elevation, with a few plants reaching as far up as 3400 meters. The lowermost elevation known for plants of *C. bella* is 3000 meters, but most occur above 3300 meters.

The similarities between *Castilleja bella* and high elevation *C. scorzoneraefolia* suggest that some gene flow may be occurring between the two taxa. In a few collections of relatively taller plants, some plants have lobed bracts, while others have entire bracts (e.g., *Mueller & Mueller 1239*-TEX lobed but *Mueller & Mueller 1239*-GH entire; *McDonald 1695* and *Hinton 17109*, most plants with lobed bracts, few with entire). Somewhat arbitrarily, I have identified all plants from these populations as *C. bella*. On Peña Nevada, however, where *C. scorzoneraefolia* is common at lower elevations and extends upward to at least 3400 meters, the difference between it and *C. bella* is marked. No plants there of *C. scorzoneraefolia* produce lobed leaves or bracts and most of them are single or few stemmed from the base.

Castilleja bella is very similar to *C. moranensis* Kunth (=*C. pringlei* Fern. and *C. schaffneri* Hemsley), which is also primarily caespitose but shows the same variability in height as *C. bella*. *Castilleja moranensis* occurs in the states of Hidalgo, México, Morelos, Puebla, and Veracruz, where it is found in a variety of habitats in elevations ranging 2400-3700(-4000) meters. It is not clear whether *C. bella* and *C. moranensis* are sister species, with the caespitose habit and lobed floral bracts inherited from a common ancestor, or whether each species may have been independently derived from *C. scorzoneraefolia*. The two can be distinguished by the contrasts in the following couplet.

1. Calyx cinereous, the veins and lobe margins densely ciliate with stiffly

spreading, white hairs; leaves mostly 1-3 mm wide at midleaf (below the divergence of the lobes). ..... *C. moranensis*

1. Calyx green, the veins and lobe margins sparsely pilose with loosely spreading, vitreous hairs; leaves mostly 4-6 mm wide at midleaf. ..... *C. bella*

IV. The identity of *Castilleja aspera*

Castilleja aspera Eastwood, Proc. Amer. Acad. Arts 44:580. 1909. TYPE: MEXICO. Chihuahua: Sierra Madre near Colonia García, 2287 m, 3 Jun 1899, *C.H.T. Townsend & C.M. Barber 449* (HOLOTYPE: GH!).

Castilleja nelsonii Eastwood, Proc. Amer. Acad. Arts 44:579. 1909. LECTOTYPE (designated here): MEXICO. Chihuahua: Mount Mohinora, 1 Sep 1898, *E.W. Nelson 4895* (GH!; Isolectotypes: GH!, US,US-photo at GH!). The lectotype and isolectotype sheets at GH apparently hold the upper portion and base of a single plant, respectively, perhaps mounted separately by mistake.

Plants perennial. Stems erect, 18-40 cm tall, sometimes few branched from the base, invested with an understory of minute, eglandular, spreading hairs, the overstory absent or nearly so to much longer, stiffly spreading, vitreous hairs, the latter often gland tipped. Leaves sparsely and minutely scabridulous to sparsely glandular pilose, oblanceolate or narrowly oblong lanceolate to elliptic, 18-62 mm long, 5-13 mm wide, clasping to subclasping, sometimes barely so, 3(-5) veined, the veins strongly raised on the abaxial surface, margins of lower leaves sometimes with short, spreading cilia. Floral bracts entire, 3 veined, 5-8 mm wide, the uppermost red tipped. Calyces red and glandular at the apex, 18-25 mm long, tubular or narrowing toward the apex, the primary lobes 5-9 mm long, with acute apices, nearly equal in length, the secondary lobes 2-4 mm long, triangular. Corollas 20-32 mm long, the lower lip of 3, thick, green teeth ca. 2 mm long, the galea 8-12 mm long, pilose and glandular dorsally, ca. 33%-40% as long as the corolla, exserted 2-10 mm from the calyces. Chromosome number unknown.

Northern Chihuahua to central Durango (Map 2); pine-oak to pine woodlands, 2100-2670 m; Jul-Sep.

Additional collections examined: MEXICO. Chihuahua: Mpio. Bocoyna, W of Creel on mesa and E slope above Río Oteros, 1 Aug 1977, *Bye & Weber 7823* (GH); near Colonia García, 25 Aug 1899, *Nelson 6101* (GH); S of Colonia García, 23 Sep 1934, *Pennell 19131* (GH); Mpio. Guerrero, 7 mi E of Tomochic on road to La Junta and Cuauhtemoc, 5 Oct 1986, *Spellenberg et al. 8880* (TEX); near Colonia García, 4 Jun 1899, *Townsend & Barber 8* (GH,MO); near

Colonia García, 9 Aug 1899, *Townsend & Barber 250* (GH,MO). Durango: Mpio. Santiago Papasquiaro, ca. 22 air km WNW of Santiago Papasquiaro, 25 Aug 1983, *Worthington 11437* (NY).

The vestiture of *Castilleja aspera* appears to be somewhat more variable than normal for most species of the genus. The type of *C. nelsonii* represents an extreme condition with strongly reduced vestiture, the leaves only sparsely and minutely scabrid. *Worthington 11437* from northern Durango is similar to the type of *C. aspera* and other plants from around Colonia García, Chihuahua, except for *Pennell 19131* and *Bye & Weber 7823*, which are more like the type of *C. nelsonii*. Additionally, the secondary calyx lobes of *C. nelsonii* (the type) are well differentiated but not sharply acute as in the other specimens of *C. aspera*, and it was apparently solely on this basis that Eastwood separated *C. nelsonii* from *C. aspera*. Nevertheless, considering their morphological similarity in all other features, as well as their geographical identity, the two are treated here as conspecific.

Plants from southcentral Durango have been identified by Eastwood (1909) and others as *Castilleja aspera*, but in the present study, they primarily are placed with following species, which is previously undescribed.

Castilleja durangensis Nesom, *sp. nov.* TYPE: MEXICO. Durango: ca. 5 km NE of El Salto, Rte 40 near K 1059, pine woods and wet llanos, under pine trees, with *Eryngium*, *Commelina*, *Ranunculus*, *Calochortus*, and *Lobelia*, 2780 m, 6 Aug 1966, *R.W. Cruden 1160*, voucher for chromosome count of n=12 [Heckard 1968, as *Castilleja aspera*] (HOLOTYPE: TEX!; Isotype: GH!)

Castillejae asperae Eastwood similis sed vestimento eglanduloso dense brevihispidulo et foliis angustioribus absque venis valde elevatis differt.

Perennials, apparently from shallow, slender, woody rhizomes; stems, leaves, and bracts evenly and densely hispidulous with sharp pointed, spreading, sometimes slightly deflexed hairs 0.1-0.3(-0.5) mm long, eglandular. Stems erect, unbranched, 13-40 cm tall. Leaves ascending, often distinctly recurved, linear to oblong lanceolate, basally rounded and subclasping, 2-5 cm long, 2-5 mm wide, 3-(-5) veined. Mature inflorescence/infructescence (3-)6-15 cm long; floral bracts entire, narrowly oblanceolate to narrowly obovate, 3 veined, 5-8 mm wide, red tipped. Calyces red and glandular at the apex, 18-22 mm long, tubular, the primary lobes 6-7 mm long, with acute apices, nearly equal in length, the secondary lobes 1-4 mm long, triangular. Corollas 21-25 mm long, the lower lip of 3, thick, green teeth 1-2 mm long, the galea 7-10 mm long, pilose and glandular dorsally, ca. 33%-40% as long as the corolla, exserted 2-6 mm from the calyces. Chromosome number, n=12 (voucher is type collection).

Southcentral Durango (Map 2); grassy slopes, sometimes wet, in pine and pine-oak woodlands; (2300-)2500-2850 m; Jun-Sep(-Oct).

Additional collections examined: MEXICO. Durango: 32.7 mi W of Durango, well spaced pine-oak forest on gentle slopes of loamy soils over volcanic rock, 23 Jul 1955, *Johnston 2686* (TEX); 39 mi E of El Salto, 7 Jun 1967, *Moldenke 1573* (NY, mixed with *Castilleja scorzoneraefolia*); 4 mi E of El Salto on road to Durango, 22 Aug 1957, *Ornduff & Solbrig 4639* (GH); Otinapa, 25 Jul-5 Aug 1906, *Palmer 367* (GH,MO, cited by Eastwood as *C. aspera*); El Salto (Aserraderos), grassy pineland, 28 Aug 1934, *Pennell 18294* (GH-with 1 plant of *C. nervata*); Metates, N of Cueva, pineland on mt. slope, 29-30 Aug 1934, *Pennell 18393* (GH-with 1 plant of *C. nervata*); El Salto (Aserraderos), grassy pineland, 31 Aug 1934, *Pennell 18499* (GH); El Salto (Aserraderos), mossy, grassy pineland, 1 Sep 1934, *Pennell 18542* (GH); El Salto (Aserraderos), marshy glade in pineland, 1 Sep 1934, *Pennell 18549* (GH); 3 mi E of El Salto off Hwy 40, 21 Sep 1974, *Rollins & Roby 7426* (GH-with 1 plant of *C. saltensis* Eastwood, NY); 28 mi E of El Salto, 23 Jul 1976, *Walker 76H23* (MO).

The plants of *Castilleja durangensis* are confined to a small area of southcentral Durango (Map 2). They are somewhat similar in habit to *C. scorzoneraefolia*, but their evenly and densely short hispidulous vestiture, lacking glandular hairs, separates them from all other Mexican species. The secondary calyx lobes of *C. durangensis* are triangular with acute apices, a distinctive feature shared with plants of *C. aspera* and perhaps indicating a close relationship between the two. Plants of *C. aspera* are generally taller and the leaves broader than in *C. durangensis* and typically produce a vestiture more similar to that of *C. scorzoneraefolia*. The vestiture of the two branches of *Moldenke 1573* (*C. durangensis*) is slightly glandular, probably reflecting the genetic influence of nearby *C. scorzoneraefolia*, plants of which are mounted on the same sheet.

V. A new species related to *Castilleja lanata*

Castilleja galehintoniae Nesom, *sp. nov.* TYPE: MEXICO. Nuevo León. Mpio. Galeana, San José de Las Joyas, 2480 m, common on bare hillside, flowers yellow, 5 Jul 1983, *Hinton et al. 18422* (HOLOTYPE: TEX!; Isotypes: ANSM!,MEXU!,NY!,UC!).

> Differt a *Castilleja lanata* A. Gray statura breviore, bracteis ac calycibus absque apicibus rubris, et corollis brevioribus labio infero loborum longorum linearium composito.

Perennials, arising from slender, woody, rhizomelike caudex branches, the stems 5-25 cm tall; stems, leaves, bracts, and calyces evenly and densely tomentose-villous with whitish, long, minutely filiform and intertwined hairs,

at least many of these originating as lateral branches of dendritic hairs, mostly with one node and several branches, minute glands sometimes apparent but never prominent beneath the other hairs. Leaves densely arranged on the stems, linear, 3 veined, 1.5-4.5 cm long, 1.0-1.5(-2.5) mm wide. Mature inflorescence/infructescence 2-4 cm long; floral bracts 13-22 mm long, abruptly differentiated from the leaves, linear with a pair of linear, lateral lobes originating at about midlength. Calyces 15-18 mm long, tubular or slightly narrowing toward the apex, equally divided, the primary lobes 6-7 mm long, the secondary lobes rounded, barely developed, 0.5-1.0 mm long. Corollas 15-20 mm long, yellow with blackish veins, the lower lip of 3, thick, linear lobes 2-4 mm long, the galea 10-11 mm long, 50%-55% as long as the corolla, dorsally glandular but without other hairs, exserted 1-4 mm from the calyx. Chromosome number unknown.

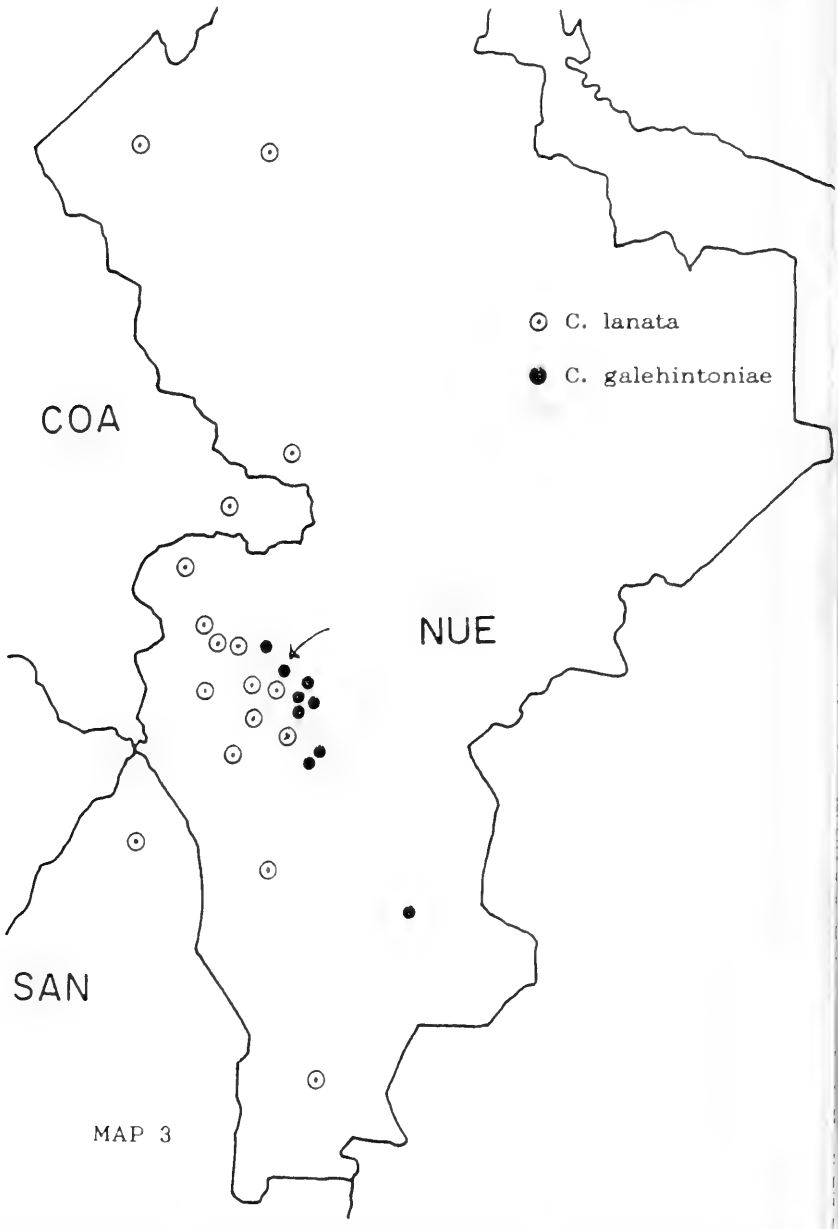
Nuevo León endemic (Map 3); apparently restricted to gypseous substrates, in matorral, grasslands, cedar savannas, open oak woods; 1300-2480 m; Apr-Aug(-Oct).

Additional collections examined. MEXICO. Nuevo León: Mpio. Aramberri, E of Aramberri, 14 May 1991, *Hinton et al. 20933* (TEX). Mpio. Galeana: above E Carrizo, 16 Oct 1983, *Hinton et al. 18149* (TEX); S slope of Potosí, 25 Jun 1983, *Hinton et al. 18449* (TEX, dup); San José Las Joyas, 23 Jul 1983, *Hinton et al. 18530* (TEX, dup); road to Dieciocho de Marzo, 11.5 mi E of jct with Hwy 57 at San Rafael, 28 mi NW of Dieciocho de Marzo, 4 Jul 1985, *Luckow 2651* (TEX); 15 mi SW of Galeana, above Encinal, 19 May 1934, *Mueller 485* (GH,TEX); ca. 15 mi SW of Galeana, Taray to Alamar at la Mesa de la Zorra, 20 Jul 1934, *Mueller 1109* (GH,TEX); Arroyo Hondo, Hacienda San José de Raices, 31 Jul 1935, *Mueller 2307* (GH,MO,TEX); Hacienda Pablillo, 1 Aug 1936, *Taylor 41* (MO,TEX); Hacienda Pablillo, 26 Aug 1936, *Taylor 221* (TEX).

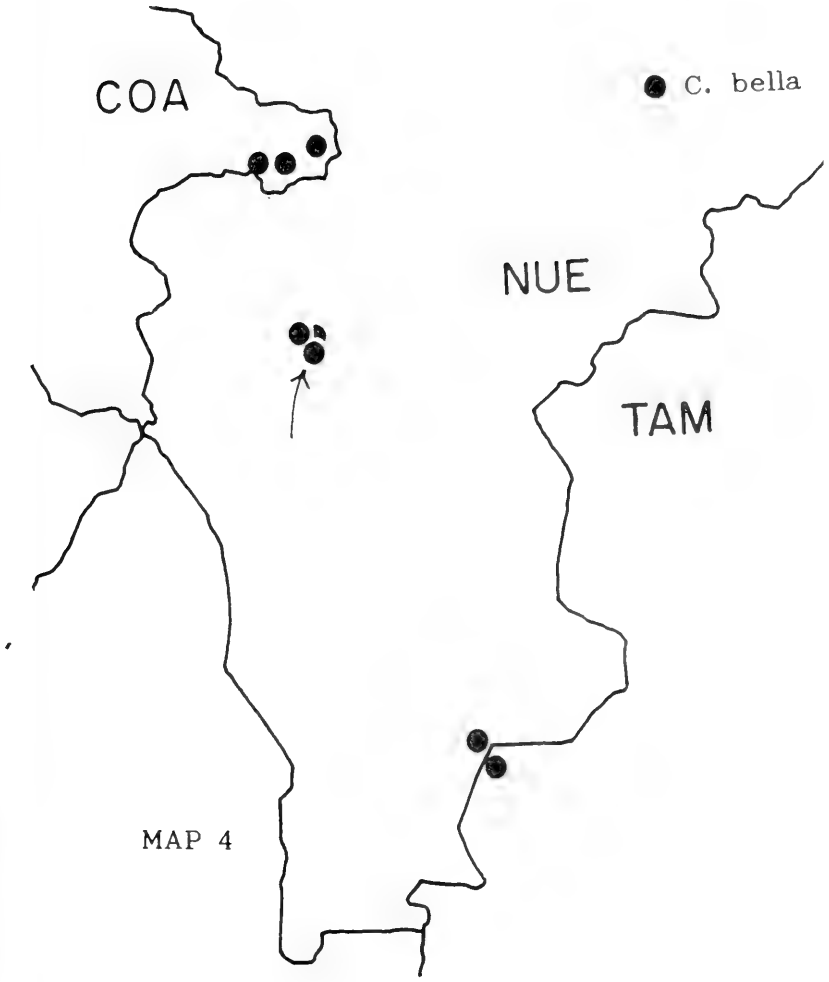
The new species is endemic to southcentral Nuevo León, México (Map 3), and it is named for Gale Hinton, daughter of Jaime Hinton and brother of George, who loved the mountains and flowers around her home in the same area of Nuevo León. *Castilleja galehintoniae* is clearly most closely related to *C. lanata*, which also produces a dense vestiture of branched hairs, mostly linear leaves, an evenly divided calyx, and corollas with a lower lip of 3 linear lobes. The two species differ in features noted in the following couplet.

1. Stems 20-100 cm tall; floral bracts with lobes usually originating from the proximal third, densely lanate basally, the apices glandular but not densely lanate; calyces 20-27 mm long, with primary lobes 10-14 mm long; corollas 22-37 mm long, the galea dorsally pilose as well as glandular. ..... *C. lanata*

1. Stems 5-25 cm tall; floral bracts with lobes usually originating from near the middle, apices densely lanate, the vestiture similar from base to tip;



Map 3. Distribution of *Castilleja galehintoniae* and *C. lanata* in Nuevo León and closely adjacent areas. Arrow shows the location of the type collection of *C. galehintoniae*; the type of *C. lanata* is from Texas.



Map 4. Distribution of *Castilleja bella*. Arrow shows the location of the type collection.

calyces 15-18 mm long, with primary lobes 6-7 mm long; corollas 15-20 mm long, the galea dorsally glandular but not otherwise pubescent. .. . . *C. galehintoniae*

While *Castilleja lanata* is somewhat variable in size, it is consistently and easily recognizable as a single species over its entire geographic range. It occurs widely in the southwestern United States (Arizona, Colorado, New Mexico, and southwest Texas) and northern México (from Sonora, Chihuahua, and northern Durango to Coahuila, northern Zacatecas, San Luis Potosí, and southern Tamaulipas). It is also relatively common in western Nuevo León, where its geographic range touches that of *C. galehintoniae*, and the two are apparently even slightly sympatric in that area (Map 3). Several collections from the area of sympatry can be identified as possible intermediates (e.g., *Cowan 4626*-TEX, near the village of El Potosí, and some plants of *Hinton 18449*-identified here as *C. galehintoniae*), but where the two taxa meet, the transition in morphology for the most part appears to be abrupt, with *C. galehintoniae* strikingly different in appearance from *C. lanata*. Putative intermediates have shorter calyces and corollas than normal for *C. lanata*, but the floral bracts and calyces are distally distinctly red with somewhat reduced vestiture. Some other collections of *C. lanata* from this area also are unusual in producing lobed upper leaves, although the origin of this variability is not clear.

VI. A new species of uncertain relationships

Castilleja dendridion Nesom, *sp. nov.* TYPE: MEXICO. Oaxaca: Dist. Centro, 10 mi NE of Oaxaca along Hwy 175, pine-oak forest on steep slopes, 2 Sep 1982, *L.E. Gieschen s.n.* (HOLOTYPE: TEX!).

A speciebus ceteris *Castillejae* dignoscenda vestimento denso trichomatum dendriticorum flavipigmentosorum, foliis confertim dispositis linearibus integrisque, bracteis floralibus lobis ad apicem expansis dentatisque, et lobis calycum pariter divisis.

Shrubby perennials, the stems basally woody and at least 40 cm tall; stems, leaves, floral bracts, and calyces densely invested with multicellular, dendritic hairs 0.2-1.0 mm high, branching 2-4 times above the 1-2 basal (stipe) cells, each hair with 2(-3) branches at each cellular node, the hairs of the stems and leaves usually prominently yellow pigmented, giving the whole plant a yellowish cast. Leaves linear-filiform, 9-17 mm long, ca. 1 mm wide, not at all basally widened or clasping, densely arranged (3-6 per cm of the stem) with axillary tufts of smaller leaves at nearly every node. Mature inflorescence/infructescence 4-10 cm long. Floral bracts abruptly differentiated from

the leaves, 14-15 mm long, 2-3 mm wide at the base, with a pair of linear-lanceolate lobes arising 2-3 mm from the base, all 3 lobes red and abruptly broadened apically, the apices truncate and shallowly toothed. Calyces red tipped and glandular, 13-15 mm long, tubular, equally divided, the primary lobes 6-8 mm long, secondary lobes deltate, ca. 1 mm long. Corollas 14-15 mm long, lower lip of 3, thick teeth ca. 2 mm long, the galea 8-9 mm long, ca. 60% as long as the corolla, dorsally glandular but without other hairs, exserted (0-)1-2 mm from the calyx. Chromosome number unknown.

Known only from the type collection (Map 1), which comprises a single, though full and densely floriferous, branch.

Castilleja dendridion is so distinctive in its morphology that no other species in the genus can be easily identified as closely related. Other species of *Castilleja* produce dendritic hairs (see Nesom 1991, as well as *C. galehintoniae*, above), but such highly elaborated hairs are not found elsewhere in the genus. Further, the peculiar morphology of the floral bracts apparently is found only in this species. The evenly divided calyx at least suggests that *C. dendridion* belongs among the species placed by Eastwood (1909) in sect. *Euchroma* (Nutt.) Benth., although the overview of the subtribe Castillejinae by Chuang & Heckard (1991) suggests that this morphology is probably primitive within the subtribe. Chuang & Heckard (1991) noted that overemphasis of the nature of calyx incision in classification probably results in the recognition of artificial groups, and they observed that satisfactory arrangement of *Castilleja* species into groups awaits a more detailed knowledge of the genus. All taxa treated in the present study are in *Castilleja* subg. *Castilleja* sensu Chuang & Heckard.

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